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Editor: JOHN M. COULTER

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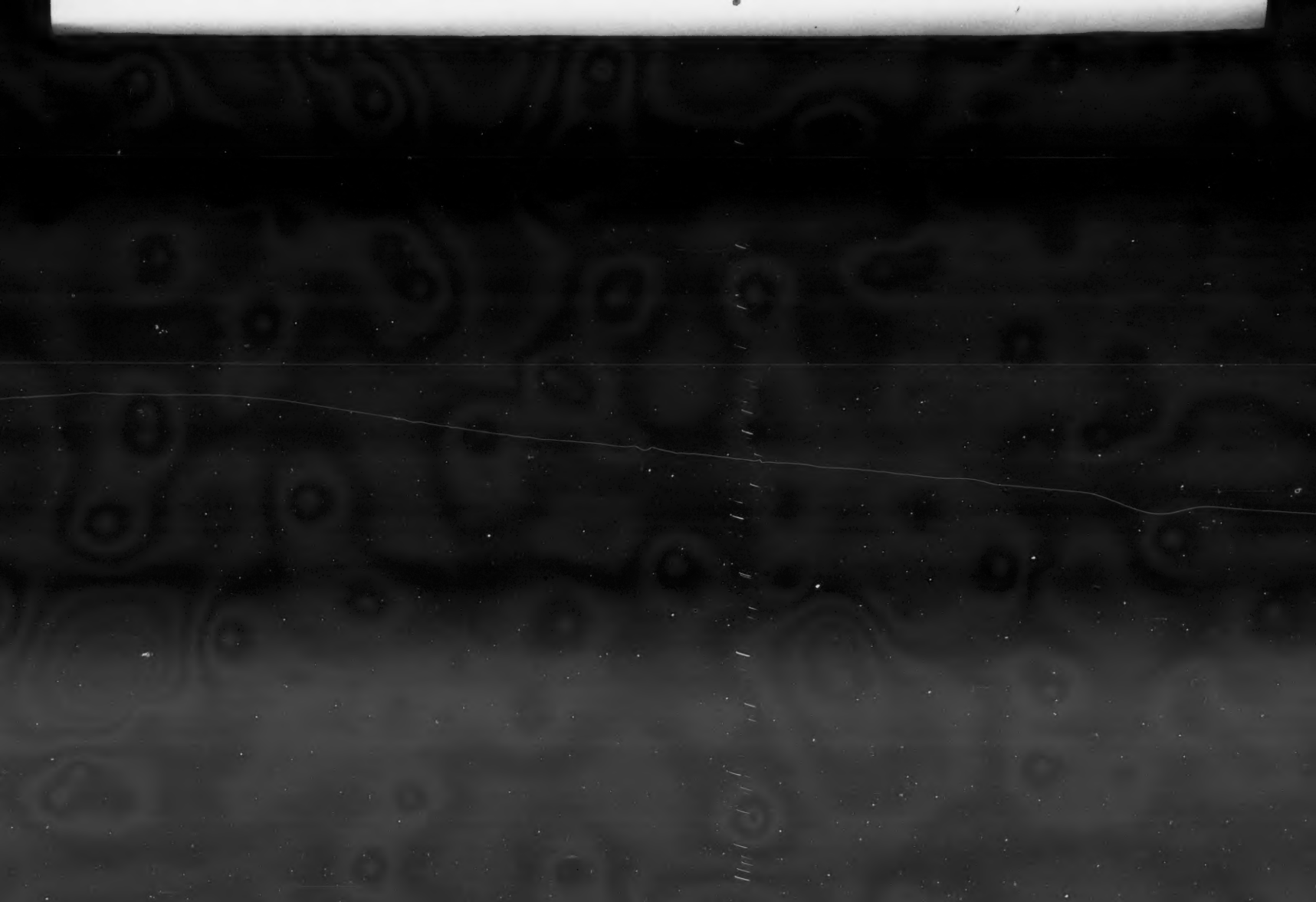

VOLUME LII NUMBER 2

THE
BOTANICAL GAZETTE

AUGUST 1911

THE ADULT CYCAD TRUNK

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CHARLES J. CHAMBERLAIN

(WITH TWENTY FIGURES)

The structure and development of the cycad seedling is fairly well known in all the genera, and in *Dioon*, *Ceratozamia*, and *Microcycas* recent investigations have been particularly thorough; but some features of the adult trunk have hitherto escaped observation, doubtless because such material is so difficult to obtain. As a matter of fact, most of the descriptions are based upon dead conservatory plants which had begun to decay and so had become worthless as ornamental specimens.

Historical

As early as 1829, BRONGNIART (1) described the stem of *Cycas revoluta*, and showed clearly that, in spite of the external habit, the woody structure was not at all related to that of palms, but resembled the wood of dicotyls, the principal difference being that *Cycas* had no bast or growth rings.

VON MOHL (2) studied a specimen of "*Zamia latifolia*" (*Encephalartos*) 1.5 meters in height, and also a section of a large trunk of *Cycas revoluta*. He recognized the bast and described the histological characters of the wood, which he found to resemble that of dicotyls, except that it lacked true vessels. In the pith he found bundles like those of many cacti. There were no growth rings.

The excellent work of METTENIUS (**3**), published in 1861, deals with *Cycas revoluta*, *Encephalartos horridus*, *Dioon edule*, and *Zamia muricata*. The course and structure of leaf traces are described in detail, and spiral vessels are noted for the first time, these having escaped the observation of previous investigators, probably because in mature stems they are lacking next the pith, where one might expect to find them. He saw bundles in the pith of *Dioon* and correctly interpreted them as belonging to the vascular system of the peduncle.

SOLMS-LAUBACH (**4**) traced the vascular supply of the peduncles in *Stangeria paradoxa* and *Ceratozamia mexicana*, and also noted the formation of phellogen in the leaf bases.

In his *Histologische Beiträge* III, STRASBURGER (**5**) describes the histological structure of a large trunk of *Cycas circinalis*, and gives a critical discussion of the literature.

In 1896, WORSDELL (**6**) made a thorough investigation of a large trunk of *Macrozamia Fraseri*. This form has a well-developed system of vascular bundles in the pith, described as not being connected in any way with peduncles. There are also concentric zones of wood, as in *Cycas*, and these, WORSDELL (**6**) believes, are remnants of some ancient structure which consisted of rings or layers of concentric vascular strands. To him the structure recalls that of the *Medullosa* stem.

From these accounts we get our conventional idea of the cycad stem, with its armor of leaf bases, thick cortex, narrow zone of wood, large pith, numerous medullary rays, and no growth rings.

Investigation

In September 1910 I was able to study in the field the adult trunks of *Dioon edule* and *D. spinulosum*, the study being facilitated by the active encouragement of Gov. TEODORO A. DEHESA, of the state of Vera Cruz. The field study was supplemented by notes and material from Mr. ALEXANDER M. GAW, of the Bureau of Information, Jalapa, state of Vera Cruz. Abundant material of *Dioon spinulosum*, accompanied by notes, was sent to me by Mr. J. C. DENNIS, superintendent of the Hacienda de Joliet, near Tierra Blanca, but in the state of Oaxaca. I am glad to acknowledge my

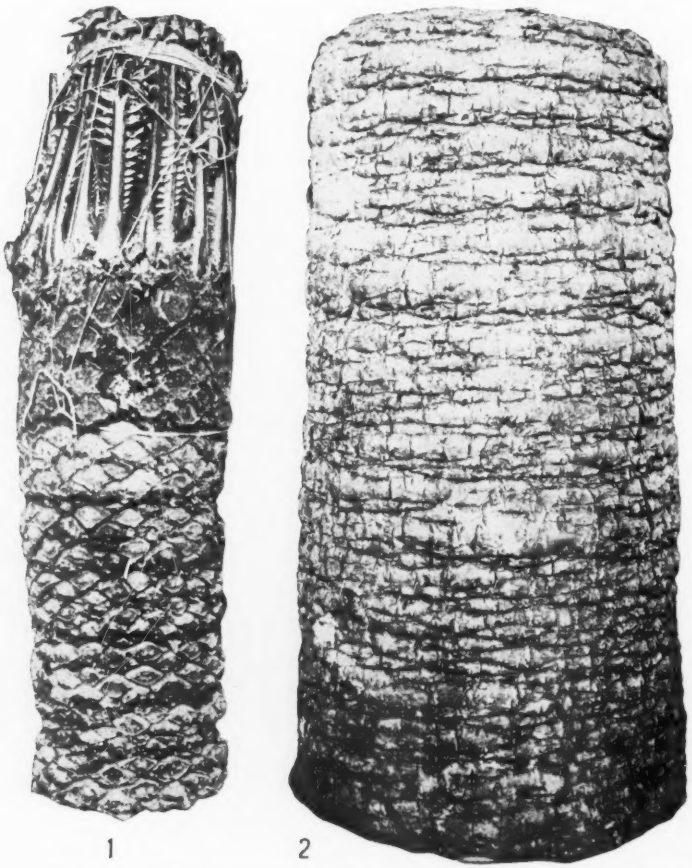
indebtedness to these gentlemen, for without their cooperation the investigation of such inaccessible material would have been impossible.

MACROSCOPIC STRUCTURE

The conventional account of the trunk is doubtless true for all young cycads and for most old ones, but it is not correct for large plants of *Dioon spinulosum*, and probably not for others which have attained any considerable height. In *D. spinulosum* the large amount of wood, the zone sometimes reaching a thickness of 10 cm., first attracted my attention, but since material was available, it seemed desirable to examine the whole trunk. Plants were studied both at Tuxtepec and at the Hacienda de Joliet, but the following account, whenever it relates to *D. spinulosum*, is based upon material from the latter locality.

AGE.—As mentioned in a previous paper (**7**), the trunk sometimes reaches a height of more than 16 meters. From the crown to the base the trunk is marked with a series of ribs due to the alternation of foliage and scale leaves, the constrictions between ribs corresponding to the scale leaves, and the ribs themselves being the larger leaf bases of the crowns of foliage leaves. Obviously, the number of crowns which a plant has borne can be determined by counting the ribs, and, assuming that a new crown is produced each year, the age of the plant would then be known. But it is not certain that new crowns are formed every year, and whether the interval is regularly two years remains to be determined. At any rate, an estimate making the number of years correspond to the number of crowns would be extremely conservative. In our previous account (**7**) the age of the tallest specimens was estimated at about 400 years, the estimate assuming a crown to be produced every other year. It was also stated that the scars are so obscure on the lower portions of the trunk that accurate counting is difficult. While this is true, we now find that the counting can be carried much farther than we had supposed, and also that the obscure ribs formed by successive crowns are very much closer together in the lower than in the upper portion of the trunk. The difference between the upper and lower portions of a trunk 6 meters in height is shown in figs. 1 and 2, the lower portion being taken

30 cm. above the surface of the rock upon which the plant was growing. The foliage display practically always consists of two successive crowns, the leaves of the lower standing transversely or beginning to droop, while those of the latest crown are more erect, but the two nevertheless presenting the appearance of a single



FIGS. 1, 2.—*Dioon spinulosum:* fig. 1, upper part of a trunk 6 meters in height; the latest crown is tied with the string, the next crown below has been cut away with a machete, and the leaves of the 6 crowns below this have fallen off naturally; $\times\frac{1}{6}$; fig. 2, lower part of same trunk, showing scars of 21 crowns; $\times\frac{1}{5}$.

crown. In fig. 1 the latest crown is tied to protect the bud, and the leaves of the crown below have been cut off. With this explanation, it will be seen that the upper portion has borne 8 crowns. The lower portion has borne 21 crowns, of which 6 or 7 toward the top are easily counted, while the rest are increasingly indistinct. How many crowns were borne by the intervening piece, about 4 meters in length, and also by the stump, is not known, but 100 crowns would be a very low estimate, and the plant would be more than 100 years old even if a new crown were produced every year.

ARMOR.—In some forms, like *Dioon edule* and *Encephalartos Altensteinii*, the armor of leaf bases is so persistent that each leaf base is distinguishable even in the lower portion of the trunk, while in *Dioon spinulosum* and others the leaf bases become indistinguishable in the lower portion of old trunks.

In *Dioon edule*, below the two green crowns constituting the foliage display and appearing as a single crown, is a crown represented by decaying midribs from which most of the leaflets have fallen, and below this will be found one or more crowns represented by irregular jagged stumps, several centimeters in length, and it is only below these that one finds the smoothly cut off bases. The reason is easily determined. As in annually deciduous dicotyls, an abscission layer of phellogen is developed, but at so late a period that only a decayed stump of midrib remains to be cut off. After the stump has fallen, a new phellogen appears a little deeper than the first, and then another, so that successive phellogens keep scaling off the outer surface, even in forms with such persistent leaf bases as *Dioon edule*. At Chavarrillo, where this species is most abundant, the trunk is often damaged by fire. In such cases, where the entire armor may be destroyed, an extensive phellogen appears in the cortex, the meristematic layer sometimes reaching a width of several millimeters, and in this way a smooth protective covering is built up.

In *Dioon spinulosum* the phellogens are more vigorous, and successive layers are scaled off until the leaf bases in the lower portion of old trunks become indistinguishable, and even the ribs due to the alternation of scale and foliage leaves become obscure. We have

never seen a specimen of *Dioon* from which all of the armor had scaled off, except in case of injury.

CORTEX.—The cortex of a large plant grows rapidly for a few years, and then during the long life of the plant grows very little. In a 6-meter specimen of *Dioon spinulosum*, at a distance of 15 cm. below the apex, the width of the zone of cortex, measured from the outer border of the phloem to the beginning of the leaf base region, was 1–1.5 cm.; while the width of the cortex near the base of the stem, where the tissues were at least 100 years older, had increased only to 1.5 or 2 cm.

Except in cases of injury, there are no meristematic regions in the cortex, *Dioon* being strictly monoxylic, and there is no growth by a phellogen at the periphery, the phellogen layers being confined to the leaf base region and not reaching the cortex itself. In forms which lose their armor through the vigorous activity of successive phellogens, the cortex itself is invaded, but in such cases the invading phellogen adds as much or more than it cuts off, and the stem may even increase in diameter.

The cortex is traversed by numerous leaf traces, some of them direct and others forming the characteristic girdle. There are also numerous mucilage canals and cavities, some of them following the course of the bundles, but most of them being independent. Crystals of calcium oxalate are numerous, and tannin cells are so abundant that a freshly cut stem changes color in a few minutes.

AMOUNT OF XYLEM.—The cycad stem has always been described as having a large pith and cortex, with a small zone of wood between them.

According to BRONGNIART (1), a specimen of *Zamia latifolia* (doubtless an *Encephalartos*), 1.5 meters in height and 20.5 cm. in diameter, had a pith 7.5 cm. in diameter, surrounded by a vascular zone 6 mm. in width, the xylem and phloem being of about equal thickness; beyond the phloem was a narrow cortex about 8 mm. in width, followed by a broad zone of leaf bases 5 cm. in width.

A few measurements which we have made recently are given below, all measurements being made at approximately the greatest diameter of the plant.

A plant of *Ceratozamia mexicana*, collected about 10 kilometers north of Jalapa, had a trunk 30 cm. high and 15 cm. in diameter. The pith, 5.7 cm. in diameter, was surrounded by a zone of zylem 3 mm. wide, with phloem 2 mm. wide, beyond which was the cortex 1.5 cm. wide, and surrounded by a heavy armor of leaf bases.

A mature plant of *Zamia floridana*, with a stem 15 cm. in height and 6 cm. in diameter, had a pith 1.3 cm. in diameter, the zones of xylem and phloem each measuring 2 mm. in width, and the cortex about 2 cm. in width. The entire armor had disappeared, and a comparatively regular phellogen had become established in the cortex.

A specimen of *Dioon edule* at Chavarrillo, with a trunk about 60 cm. in height and 21 cm. in diameter, had a pith 8.7 cm. in diameter, the zones of xylem and phloem each measuring 5 mm. in width, the cortex 2 cm., and the leaf bases 3.6 cm. A taller specimen, about 1 meter in height, but with the same diameter, had the following dimensions: diameter of pith, 6.9 cm.; width of xylem, 1.5 cm.; width of phloem, 8 mm.; width of cortex, 3.2 cm.; width of leaf base region, about 1.5 cm.

These measurements may be regarded as typical of most monoxylic trunks. The mount of wood in polyxylic trunks, though somewhat greater, is still so scanty that no exception to the conventional description has been necessary.

Naturally, it was with considerable surprise that I noted, in the Tierra Blanca region, trunks of *Dioon spinulosum* with zones of wood 4, 6, and even 10 cm. in width. A specimen 6 meters in height, and 33 cm. in diameter at a distance of 30 cm. above the rock on which it was growing, had a zone of wood 10 cm. in width. The phloem was 1.4 cm. in width, the cortex 2.5 cm., and the armor near the base of the plant, where it had been greatly reduced, only 0.5 to 1 cm. The pith at a distance of 60 cm. below the apex was 8 cm. in diameter, and from this point to the base of the plant its diameter was uniform. What the extent of the wood in a specimen 15 or 16 meters in height might be, remains to be determined.

The numerous large medullary rays reaching from the pith to the cortex are a conspicuous feature of the transverse section (fig. 3). Besides the large rays there are much more numerous small

ones. Both kinds of rays have a comparatively slight longitudinal extent. Each large medullary ray contains a leaf trace bundle, but the small rays are in no way connected with bundles.

GROWTH RINGS.—*Dioon spinulosum* has well-developed growth rings, a feature which, so far as I know, has not been described for any cycad. These rings are conspicuous in the upper part of the trunk, and can be recognized even in the lower portions of old plants (figs. 3 and 19). That the rings are growth rings, and that

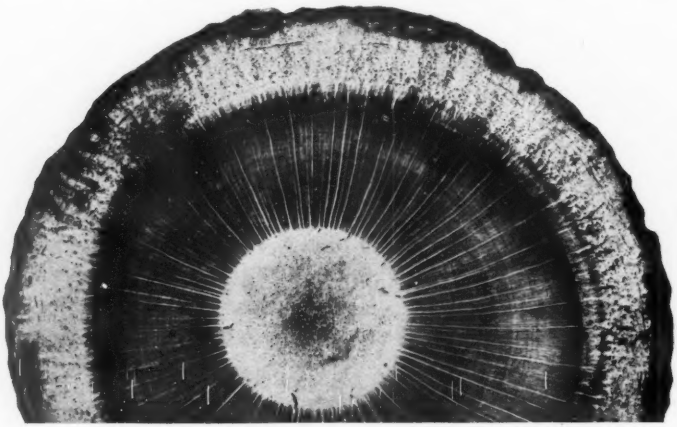


FIG. 3.—*Dioon spinulosum:* transverse section of lower part of the piece shown in fig. 2; note the large and small medullary rays, the growth rings, and the large amount of phloem; $\times\frac{1}{3}$.

they have approximately the same structure as the annual rings of dicotyls, is obvious from a glance at a transverse section; but that they are annual rings is doubtful even in *Dioon spinulosum;* and in *D. edule,* where the rings are equally conspicuous, it is absolutely certain that they are not formed annually.

A transverse section of the 6-meter plant of *Dioon spinulosum,* already mentioned, at the level of the third crown from the apex, showed four growth rings. This piece had borne one cone. A section of the same plant at the level of the eighth crown below the apex showed 13 growth rings. During the formation of the nine crowns the plant had produced at least 8 cones.

The number of rings, counted 30 cm. above the ground in the 6-meter specimen, was about 150. The number of crowns, at a very low estimate, was about 100. Any estimate of the number of cones would necessarily be very uncertain, the only data being that the first cone was borne when the plant was 1 meter in height, and that a piece 25 cm. in length, taken near the top of the plant, had borne 6 cones. Estimated only upon this data, the number of cones would have been more than 100, but the estimate is doubtless much too high, because ovulate cones are comparatively infrequent on small plants.

The number of rings, then, does not correspond exactly to either the number of crowns or the number of cones, or to the number of both combined. It is certain that in some seasons a plant produces a crown of leaves but no cone; and that it may produce a cone and no leaves; and, further, that it may produce both a new crown and a cone the same season, or it may fail to produce either a crown or a cone. It is quite probable that when either a crown or a cone is produced, a ring is formed, and that when both a crown and a cone are formed the same season, only one ring is produced.

We are inclined to believe that a period of vigorous growth, which would result in the formation of a new crown or cone, would produce also a growth ring, and that seasons which pass without the formation of a crown or a cone would not be marked by growth rings, the mere alternation of rainy and dry seasons not being sufficient for the formation of a ring in *Dioon*. If the number of rings should correspond somewhat approximately to the number of seasons, we should regard the correspondence as a coincidence, the crown and cone production being the determining factor. Of course, it is well known that dicotyls in such localities have seasonal growth rings.

In *Dioon edule* the growth rings present a very different problem, for it is certain that they correspond to neither the number of crowns, number of cones, nor number of seasons. At Chavarrillo, a plant 60 cm. in height and 20 cm. in diameter showed, in a transverse section near the base, a zone of wood 15 mm. in width. The number of rings was about 20, but the age of the plant, at a very conservative estimate, could not have been less than 100 years,

nor the number of crowns less than 50, so that whatever the factor may be which produces the ring, it must appear at widely separated intervals. The trunk is obscurely ribbed, but the ribs do not correspond to the number of crowns, many crowns being represented in each rib. It is possible that these ribs are due to the resting periods during which neither crowns nor cones are produced. The number of rings may correspond to the number of these resting periods. It is possible that such resting periods may result in the formation of new zones of wood in polyxylic stems, like *Cycas revoluta*, and only in the formation of rings in *Dioon edule*. In either case, it would require time and some vandalism to secure evidence.

CONE DOMES.—Vascular bundles in the pith have doubtless been seen by everyone who has cut a section of any mature cycad stem, but METTENIUS (**3**), studying *Dioon edule*, was the first to interpret these bundles as the vascular system of the cones. Later, SOLMS-LAUBACH (**4**) made a more thorough study of the pith bundles in *Ceratozamia*, and showed conclusively that the cycad trunk is a sympodium. Still later, the mode of development of the sympodium was described by Miss F. GRACE SMITH (**8**), who studied the origin of young cones and stem apices in *Zamia floridana*.

We have studied the pith bundles in *Dioon spinulosum*, *D. edule*, and *Zamia floridana*. In longitudinal sections of the stem, the bundles are in the form of a convex diaphragm, but since they really form a dome with the peduncle of the cone at its apex, we shall call the system of bundles a *cone dome*.

The longitudinal section shown in fig. 4 contains five cone domes, the second of which, counting from the top, is cut through the axis of the peduncle, and the third and fifth show clearly the position of the peduncle, and the other two indicate its approximate location by a thickening of the bundles. In *Zamia floridana* the appearance is similar, but in *Dioon edule*, on account of the very slow growth, a single transverse section may show parts of as many as three cone domes.

In transverse section the cone dome appears as a circle of vascular bundles more or less eccentric if cut near the peduncle, but concentric near the stele (fig. 5).

As soon as a cone begins to develop, a new meristem appears very close to the peduncle, and this new meristem may form successive crowns of leaves, but sooner or later it becomes transformed into a cone, which is really only a highly modified crown of leaves

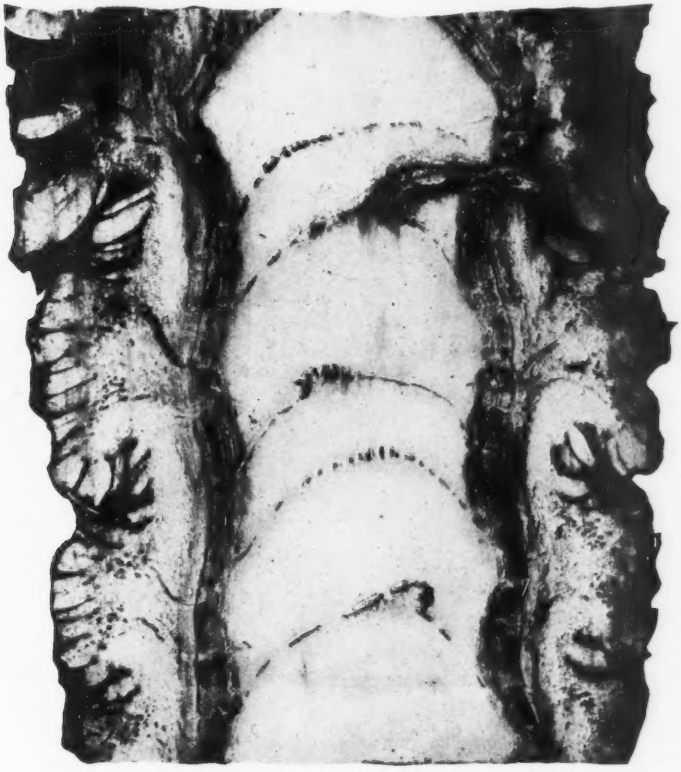


FIG. 4.—*Dioon spinulosum:* longitudinal section near the top of the piece shown in fig. 1; note 5 cone domes and, at the tip, a part of another; three ribs and parts of two more are shown; between the ribs are scale leaves; ×½.

terminating the growth of its axis. The process is then repeated. An instructive view of this phase is seen in fig. 6. A little to the right of the center is the peduncle of a large ovulate cone, and at its left is the new growing point which has produced a crown of foliage

eaves, and a crown of scale leaves appearing as a whitish triangular cluster in the figure, while the growing point itself is becoming transformed into a cone, a fact evidenced, as yet, only by a slight elongation, the point, while producing only vegetative leaves,

FIG. 5.—*Dioon spinulosum:* transverse section at about the level of the top of fig. 4; the innermost ring is the cone dome; beyond this is the vascular cylinder, with the xylem (quite dark) and the phloem (much lighter) about equal in width; the girdle leaf traces (*l*) are prominent; ×½.

being convex or at most hemispherical. Young cones of *Zamia* also may be distinguished from vegetative growing points, even before any appearance of sporophylls, by the elongation.

As the new apex develops, the old peduncle is pushed aside, new tissue gradually surrounds its base, and finally whatever

remains of the old peduncle is covered over, somewhat as in the case of a dead branch of a dicotyl. The apex of the cycad stem is remarkably broad and flat, a feature which expedites the burying of the peduncle by the new tissue (fig. 6).

FIG. 6.—*Dioon edule:* longitudinal section of the apex of a large trunk, showing three cone domes, the lowest with bundles in transverse section, the middle one with bundles going to the peduncle of a large cone, and the upper terminating in the latest apex; $\times\frac{2}{3}$.

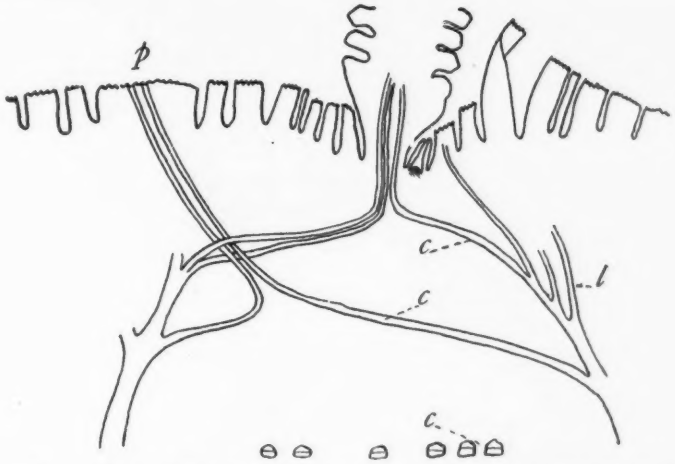
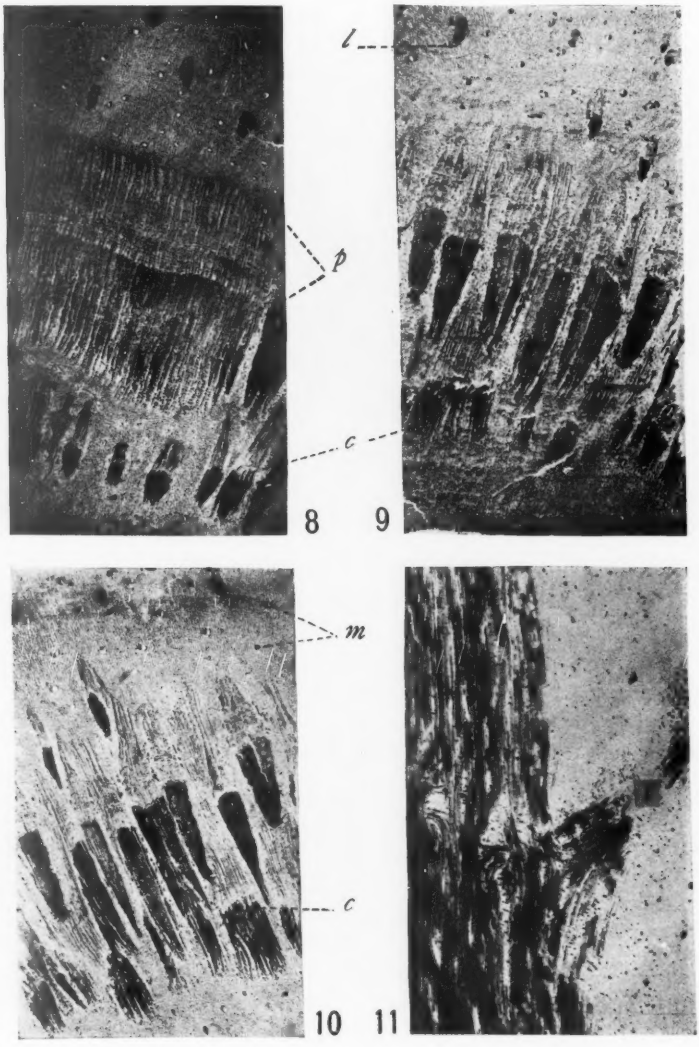


FIG. 7.—*Zamia floridana:* longitudinal section of apex of a large plant, showing three cone domes (*c*), the lower with bundles in transverse section, the middle with bundles running to the peduncle (*p*) of a mature cone, and the upper with bundles running to a young cone; the new growing point is at the right of the young cone; several leaf traces (*l*) are shown; $\times 3$.



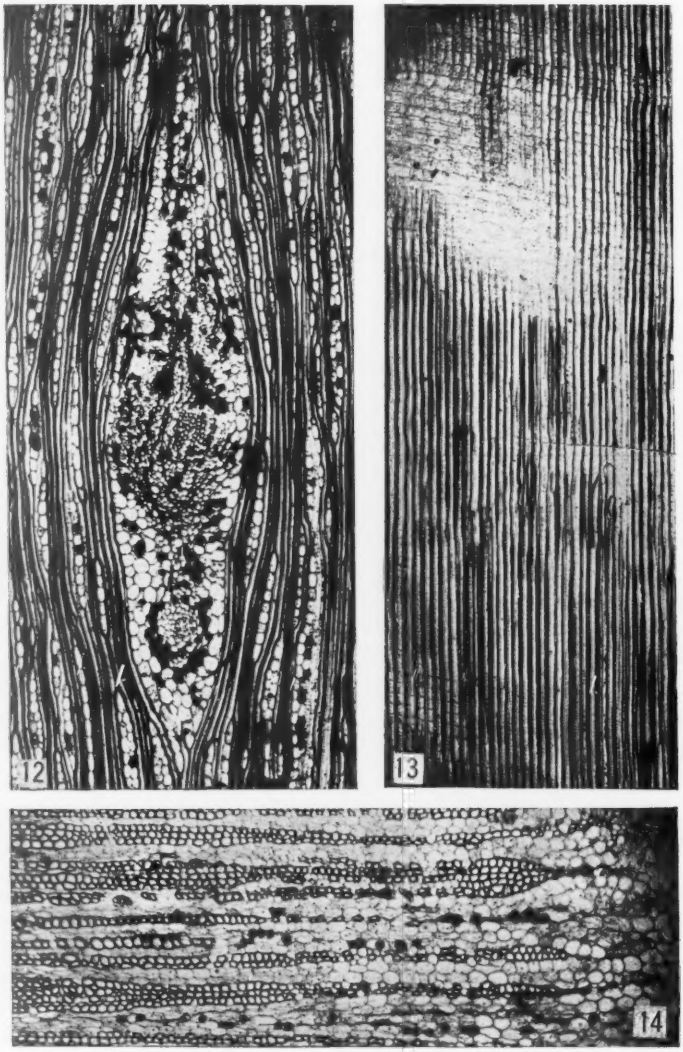
FIGS. 8–11.—*Dioon spinulosum: c*, cone domes; *m*, mucilage ducts; *l*, leaf traces; *p*, phloem; fig. 8, cone dome still separated from the main body of the stele; fig. 9, section at the union of cone dome and main body of stele; fig. 10, slightly more intimate union; fig. 11, longitudinal view of cone dome at point of union with main body of stele; all ×5.

The vascular connections are rather complex. Naturally, each cone dome must, at some point, surround the apex of the preceding cone dome. The general course of the bundles may be seen in fig. 7, which shows three cone domes, the lowest shown in transverse section, the next terminating in the base of an old peduncle, and the upper one passing into a young cone, while at the right of the young cone is the new growing point. It is evident from this figure and the preceding one that the traces of foliage leaves first touch the stele at its periphery, while the bundles of the cone domes are on the inside.

As long as the new dome is separated from the rest of the vascular tissue by a zone of pith, a transverse section looks like a section of a polyxylic stem, except that the smaller zone of vascular tissue is inside (fig. 8); but a little farther down, a transverse section presents a confused array of bundles (figs. 9 and 10). After the bundles of the cone dome and those of the previously formed wood have become arranged into a fairly regular zone, a cambium is established, and the formation of secondary xylem and phloem begins. In uniting with the previously formed wood, the course of the various strands of a bundle is not uniform, some going up, some down, and others entering more or less transversely (fig. 11).

It follows necessarily that every cycad which bears terminal cones must have cone domes in the pith. This would include all the living cycads, with the single exception of the ovulate plant of *Cycas*, in which the sporophylls are borne in a loose crown like the foliage leaves, and the growing point is not transformed into a cone, but remains meristematic. It is possible that in specimens of *Encephalartos*, which produce several cones in a circle, the meristem remains as in *Cycas*. In such a case, no cone dome would be formed; but if at any time such a plant should produce only one cone, or two or more cones in a cluster, a dome would be formed.

In *Macrozamia Fraseri*, WORSDELL (**6**) found numerous bundles in the pith, but claimed that they had no relation to cones. This species usually bears only a single cone, and consequently must have cone domes in the pith. It is possible that WORSDELL'S plant, being a greenhouse specimen, may never have produced a cone, but *Dioon edule*, which elongates very slowly, may show as



FIGS. 12–14.—*Dioon spinulosum:* fig. 12, longitudinal section of mature wood, showing apparently compound nature of the large ray at the upper portion, the bundle at the middle, and mucilage duct lower down; the dark spots are calcium oxalate crystals; fig. 13, longitudinal radial section; fig. 14, transverse section; all ×25.

many as three cone domes in a single transverse section of the trunk, and the arrangement of pith bundles resembles that described for *Macrozamia*. Since the question would be settled by a glance at a longitudinal section of a cone-bearing *Macrozamia* trunk, it is hardly worth while to speculate.

HISTOLOGICAL STRUCTURE

The living trunk of *Dioon spinulosum* cuts rather easily with an ax or machete, but is amazingly difficult to saw. Microtome sections of fresh material are not hard to cut, but transverse and longitudinal sections are likely to break at the large fragile medullary rays. A general view of the histology of the wood is shown in figs. 12–14.

XYLEM.—The xylem, in the older parts of the stem, consists principally of very long tracheids, and is traversed by large and small medullary rays.

Some writers state that there is no protoxylem in the adult cycad trunk, but the statement obviously rests upon a mistaken notion as to the character of protoxylem, such writers assuming that only spiral and annular vessels should be entitled to the name, instead of applying the term to the first xylem differentiated in a bundle, without respect to the character of the markings on the cell walls. The adult stele of *Dioon spinulosum* is endarch, and the protoxylem consists of scalariform tracheids which pass gradually into the pitted tracheids with pointed ends, constituting the principal mass of the xylem. The transition is unmistakable, the scalariform markings, elongated pits, and typical bordered pits sometimes being found in a single tracheid. The bordered pits are multiseriate, two, three, and even five or six rows being found in a radial view of a tracheid, so that in radial sections the wood might be mistaken for that of *Araucaria* (fig. 15). Pits are occasionally found on the tangential walls, but they are not numerous and are irregularly scattered.

Besides the tracheids with pointed ends, the xylem contains elongated cells with transverse walls (figs. 12 and 15–17). These at first are thin-walled and contain starch, but later may or may not become lignified and pitted. They are not uniform in length

or constant in position, although they are most numerous in contact with the medullary rays (fig. 12). That their origin is the same as that of the ordinary pitted tracheid is seen at once in a transverse section of the wood (fig. 17).

Still another form of tracheid is found in the large medullary rays (fig. 18). These tracheids are scalariform, are irregular in outline, and are nearly erect at their upper end, but become nearly

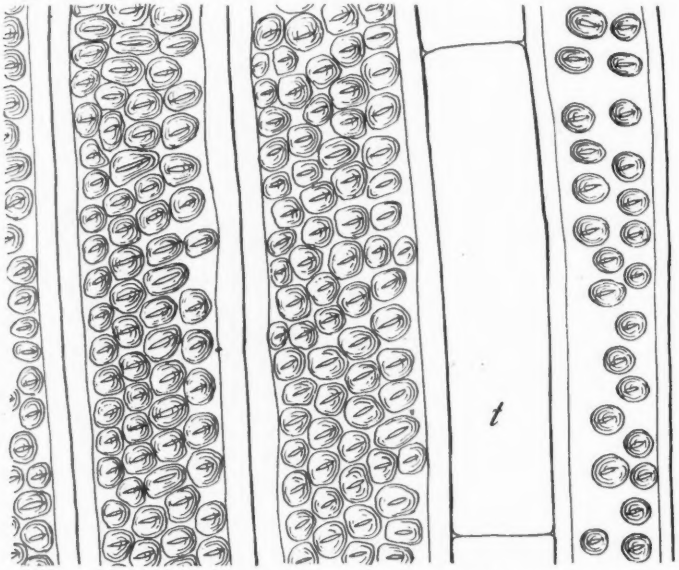
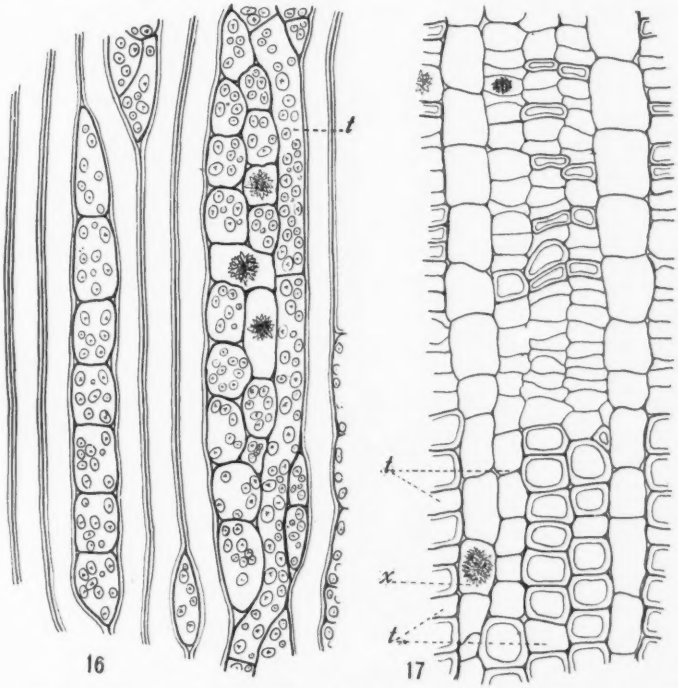


FIG. 15.—*Dioon spinulosum:* longitudinal radial section of mature wood showing multiseriate bordered pits, and also one of the thin-walled cells (*t*) of the xylem; ×390.

horizontal deeper down in the ray, so that a tangential section of the ray shows them in both longitudinal and in transverse section. Every large medullary ray would show these peculiar tracheids at some point or other, and they are particularly numerous near the pith. They connect the leaf trace bundle, which is found in every large ray, with the secondary xylem, a connection hitherto unknown in cycads. Such a secondary connection of the leaf trace is a prominent feature in angiosperms. Professor R. B. THOMSON examined preparations of the large medullary rays, and

I am indebted to him for the suggestion in regard to their connections.

The growth rings, to the naked eye, appear almost as distinct as in dicotyls, but under the microscope they are not so conspicuous (figs. 19 and 20). The latter figure presents one of the most con-



FIGS. 16, 17.—*Dioon spinulosum:* fig. 16, longitudinal tangential section of mature wood, showing thin-walled cells of the xylem (*t*) containing starch, the xylem tracheids, and the small medullary rays containing starch and calcium oxalate crystals; fig. 17, transverse section showing the phloem with several thick-walled cells, xylem with thick-walled tracheids and several of the thin-walled cells (*t*); *x*, calcium oxalate crystal in medullary ray; both ×125.

spicuous rays which could be found. In *Dioon edule*, the rings appear about the same to the naked eye, but under the microscope are quite distinct, and seem to differ considerably from those of *D. spinulosum*, as might be expected from the description given in

connection with the number of rings. I have not yet found time to give them a careful study. In the plant of *Ceratozamia*, already referred to, the cells of the xylem are quite uniform, there being no trace of growth rings, and a similar condition was found in several stems of *Zamia floridana*.

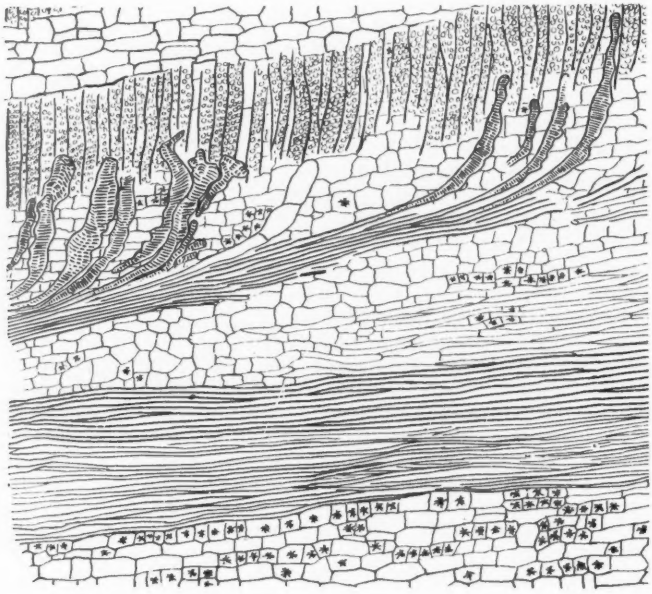


FIG. 18.—*Dioon spinulosum:* portion of large medullary ray, showing the tracheids indicated in tangential section at the tip of the large ray in fig. 12; somewhat above the scalariform tracheids are pitted tracheids of the secondary wood; the lower third of the figure shows part of the leaf trace bundle in the ray; many cells contain calcium oxalate crystals; ×40.

PHLOEM.—The phloem was overlooked by BRONGNIART, doubtless on account of its great extent and the numerous bast fibers which makes it resemble the wood. A small portion of the xylem, the cambium, and a small portion of the phloem of *Dioon spinulosum* are shown in fig. 17. The extent of the phloem is indicated in the photomicrographs (figs. 3, 4, and 8–10). In longitudinal section, especially in tangential section, the resemblance to the wood is

even more striking, the medullary rays being just the same, and the bast fibers having about the same arrangement as the long tracheids of the xylem. This structure makes the phloem nearly as rigid as the wood.

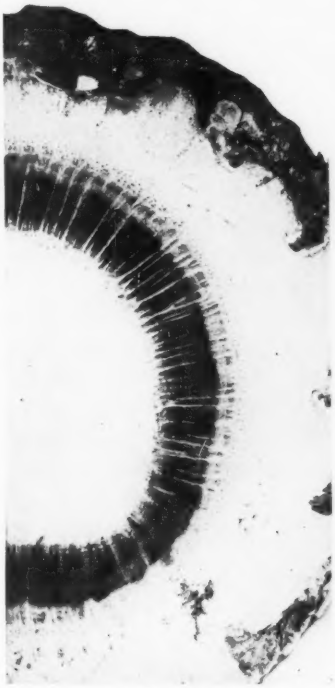


FIG. 19

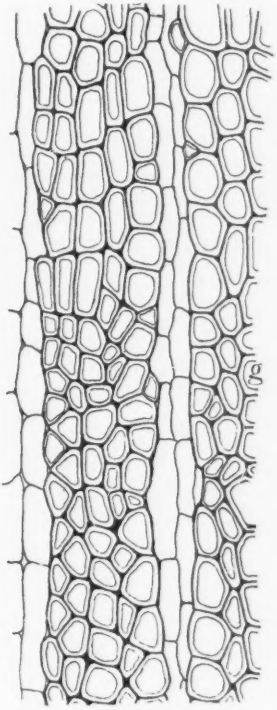


FIG. 20

FIGS. 19, 20.—*Dioon spinulosum:* fig. 19, photograph showing growth rings, $\times\frac{3}{4}$; fig. 20, a single growth ring (*g*); $\times 125$.

RAYS.—In a transverse section the large medullary rays are as conspicuous as those of *Quercus*, and the small rays, while not nearly so conspicuous, are readily visible to the naked eye (fig. 3).

The small rays vary greatly in longitudinal extent, some showing only a single cell in tangential section, while others may show more than 50, and may reach a width of 3 or 4 cells. The great

majority of the small rays are less than 20 cells in longitudinal extent, and are one or two cells wide, often two cells wide in the middle and one cell wide at both ends (fig. 12). Radially, the rays extend from the pith to the cortex, few if any new rays being formed as the trunk grows. Most of the cells contain large starch grains, but some have crystals of calcium oxalate, which is also abundant in the phloem, cortex, and pith.

The large rays also extend from the pith to the cortex. Longitudinally, they measure 4 to 8 mm., and from a width of about 1 mm. in the middle they taper to a single cell above and below. In each large ray is a leaf trace, with its phloem more or less disorganized. The xylem of this bundle is usually uppermost, but the orientation is various until the bundle reaches the cortex, where it becomes a part of the characteristic girdle. From both the pointed ends, tracheids extend into the ray, often making nearly half of the ray look like a group of small rays (fig. 12). Most of these tracheids which extend into the rays are scalariform, but some are slightly pitted, and some are the cells of the wood with transverse walls already described. Every large ray has at least one mucilage duct, and surrounding it at a distance of a few cells, the calcium oxalate crystals are particularly abundant.

While the large ray, especially in tangential section, resembles the broad ray of *Quercus*, as described by EAMES (9), its mode of formation is different, the broad ray of *Quercus* originating by the fusion of small rays, while in *Dioon* the broad ray owes its origin to the leaf trace which it contains. The tissues simply grow around the leaf trace, and the compound appearance of the ray, shown at the upper end of the photomicrograph (fig. 12), is a secondary, not a primary feature.

COMPARATIVE HISTOLOGY.—The trunks of *Dioon spinulosum*, *D. edule*, *Ceratozamia mexicana*, and *Zamia floridana* have some histological characters in common, and it is probable that all the Cycadales have enough histological peculiarities to identify the order by the structure of the trunk. The four species mentioned above are easily distinguished from each other by such histological characters, but it is very doubtful whether nearly related species of a large genus like *Zamia* could be so distinguished from each

other. The distinction would doubtless be mu more difficult in young trunks than in old ones.

The structure of the trunk of *Dioon spinulosum* is remarkably like that of the Bennettitales. The growth rings resemble those of *Cycadeoidea Jenneyana*, as described by WIELAND; the phloem, with its numerous thick-walled fibers in transverse section, is very similar to that of *Cycadeoidea Wielandi;* and the xylem, as it abuts upon the pith, also resembles that of *Cycadeoidea*. But there are also contrasting features; the broad medullary rays are not figured in the Bennettitales, and in the xylem cells with transverse walls seem to be lacking.

Summary

1. The paper deals with field material of adult stems of *Dioon spinulosum*, *D. edule*, *Ceratozamia mexicana*, and *Zamia floridana*, particular attention being given to *Dioon spinulosum*.

2. In *Dioon spinulosum* the xylem zone in a plant 6 meters in height reaches a width of 10 cm., far exceeding the extent of any xylem zone previously described for any cycad.

3. *Dioon spinulosum* and *D. edule* have growth rings, which in *D. spinulosum* correspond to the periods of activity which result in the formation of crowns or cones, but which in *D. edule* do not correspond to such periods. No growth rings were found in *Ceratozamia mexicana* or *Zamia floridana*.

4. Cone domes in the pith were studied in the four species.

5. The histological character of the adult stem was studied in *Dioon spinulosum*. The protoxylem consists of scalariform tracheids, from which there is a gradual transition to the tracheids with multiseriate bordered pits, constituting the principal part of the wood. There are also cells with the same origin as the pitted tracheids, but with transverse walls which may remain thin-walled and contain starch or may become lignified. Besides the leaf trace bundles, scalariform tracheids are found in the large medullary rays.

6. Both in the general appearance of the transverse section and in histological characters the adult trunk of *Dioon spinulosum* resembles that of *Cycadeoidea*.

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A BOTANICAL SURVEY OF THE HURON RIVER VALLEY

VIII. EDAPHIC CONDITIONS IN PEAT BOGS OF SOUTHERN MICHIGAN

GEORGE PLUMER BURNS

(WITH EIGHT FIGURES)

In a paper read before the Society for Plant Morphology and Physiology at the Philadelphia meeting (1904), the author called attention to the fact that the plants in peat-forming lakes near Ann Arbor, Michigan, are by no means all xerophytic. With xerophytes are found many plants whose structure is either mesophytic or hydrophytic, and the conclusion was drawn that in the vicinity under consideration one should no longer refer to a peat bog, as such, as a xerophytic habitat (**2**).

TRANSEAU (**17**), in a very interesting paper dealing with the distribution of bog and swamp plants, stated that the two were found growing together in the bogs of southern Michigan, and accounted for the present mixture of the two kinds chiefly on historical and climatic grounds.

PENNINGTON (**13**) concludes that the bogs in southern Michigan are heterogeneous habitats and demand detailed study.

LIVINGSTON (**12**), DACHNOWSKI (**7, 8**), and TRANSEAU (**18**) in experimenting with bog water have found that it is not the same in all zones. The samples of water taken for experimental purposes were generally from under *Larix*, *Drosera*, *Sarracenia*, *Andromeda*, *Cassandra*, *Vaccinium*, *Eriophorum*, etc., that is, from zones with marked xerophytic plants.

The distribution and position of zones of plants in the bogs of southern Michigan have been given by DAVIS (**9**), TRANSEAU (**18**), the author (**3, 4**), and others. On the side of greatest depth the following zones are found:

I. *Zone of submerged plants.*—Plants in this zone usually do not go to great depths. In many lakes no vegetation is found at a depth of 12 feet (3.66 m.). The chief plants are *Chara*, *Cera-*

tophyllum demersum, *Naias flexilis*, *Potamogeton lucens*, *P. natans*, *P. zosteraefolius*.

II. *Zone of water lilies*.—This zone is confined to shallow water seldom over 5 feet (1.5 m.) in depth. The characteristic plants are *Castalia odorata*, *Nymphaea advena*, *Brasenia Schreberi*.

III. *Zone of floating sedges*.—The mat formed by these sedges is very firm and usually about 18 inches (45.8 cm.) in thickness. The chief mat-forming plants are *Carex filiformis* and *C. oligosperma*. Associated with these, some playing an important part in mat-formation, are *Menyanthes trifoliata*, *Dulichium arundinaceum*, *Eriophorum viridi-carinatum*, *Drosera rotundifolia*, *Aspidium Thelypteris*, *Onoclea sensibilis*, *Equisetum limosum*, *Eupatorium purpureum*, *E. perfoliatum*, *Mentha arvensis* var. *glabrata*, *Scutellaria galericulata*, *Utricularia* sp., *Calopogon pulchellus*, *Campanula aparinoides*, *Arethusa bulbosa*, *Galium trifidum*, *Aster junceus*, *Potentilla palustris*, *Solidago serotina* var. *gigantea*, *Lysimachia terrestris*, etc.

IV. *Zone of bog shrubs*.—The characteristic plants of this zone are *Chamaedaphne calyculata*, *Andromeda polifolia*, *Betula pumila*, *Nemopanthes mucronata*, *Sarracenia purpurea*, *Vaccinium Oxycoccus*, *V. macrocarpon*.

V. *Zone of tamaracks*.—The principal plants are *Larix laricina*, *Cornus stolonifera*, *Osmunda regalis*, *O. cinnamomea*, *Rhus Vernix*, *Aster junceus*. In areas where the tamarack is thick there is no undergrowth.

VI. *Zone of poplars and maples*.—This zone is often of great width for reasons pointed out in a previous paper (**4**), and has the greatest variety of species of any zone. Some of the plants found are *Acer rubrum*, *A. saccharinum*, *Populus tremuloides*, *P. grandidentata*, *Prunus serotina*, *Quercus rubra*, *Q. bicolor*, *Sambucus canadensis*, *S. racemosa*, *Salix discolor*, *S. rostrata*, *Spiraea salicifolia*, *Cornus stolonifera*, *Ilex verticillata*, *Cephalanthus occidentalis*, *Rosa carolina*, *Epilobium adenocaulon*, *Verbena hastata*, *Solanum Dulcamara*, *Polygonum sagittatum*, *P. hydropiperoides*, *Geum rivale*, *Rumex britannica*, *Impatiens biflora*, *Viola blonda*, *Solidago canadensis*, *S. graminifolia*, etc.

VII. *Zone of marginal willows*.—*Salix nigra*, *S. lucida*, *S. dis-*

color, *Cornus stolonifera*, *Ilex verticillata*, *Rubus idaeus* var. *aculeatissimus*, *R. hispidus*, *R. villosus*, *Rosa carolina*, *Vitis vulpina*, *Alisma Plantago-aquatica*, *Acalypha virginica*, *Agrostis alba*, *Bidens cernua*, *Cicuta bulbifera*, *Carex vulpinoidea*, *C. scoparia*, *Eleocharis tenuis*, *Eupatorium perfoliatum*, *Geum strictum*, *Glyceria nervata*, *Juncus effusus*, *Lycopus americanus*, *L. virginicus*, *Lactuca canadensis*, *Ludvigia palustris*, *Pilea pumila*, *Polygonum Hydropiper*,

FIG. 1.—First Sister Lake near Ann Arbor, Mich.; the photograph shows the zonal arrangement of plants at the southwest corner; five zones can be distinguished as follows: water lily, bog sedge, bog shrub, tamarack, maple-poplar; the adjacent uplands are covered with oak-hickory woods; photograph by STEELE.

P. sagittatum, *Penthorum sedoides*, *Ranunculus pennsylvanicus*, *R. scleratus*, *R. delphinifolius*, etc. (fig. 1).

A study of the partial lists given above shows that they are not all xerophytes. There are at most only three zones which have bog flora as the characteristic plants. These are the floating sedge, the bog shrub, and the tamarack zones. In the first of these only those plants rooting deep in the mat can be called bog xerophytes; those rooting in the surface layers are hydrophytes. The other zones are occupied by hydrophytes or mesophytes.

The flora of the postglacial lakes studied in southern Michigan may be classified thus:

Vegetation in postglacial lakes	Hydrophytes	Submerged plants
		Water lilies
	Xerophytes	Floating sedges
		Bog shrubs
		Tamaracks
	Hydrophytes or mesophytes	Poplar-maples
	Hydrophytes	Marginal willows

An investigation has been carried on for several years by the author and some of his advanced students to determine as far as possible the edaphic conditions in the different areas outlined above. A short report has been given (**5**) and a more detailed account of some of the results is given in this paper.[1]

Temperature

The aerial parts of the bog plants are subjected to great extremes in temperature. Situated, as they are in the area under discussion, in low basins with often very steep sides, the air from the adjacent uplands drains into them, producing a temperature several degrees lower than that on the surrounding uplands during the night and early morning. During the day, however, very high temperatures have been recorded. Such temperatures have also been recorded by GANONG (**10, 11**) in New Brunswick.

Unless otherwise stated in the text, all temperature readings given in this paper, both for soil and air, were taken with Richard Frères, Paris, thermographs belonging to the University of Michigan. These instruments are shown in fig. 2 in the shelter in which they were kept in the field. The one on the left records the air, the other the soil temperatures. It was found, unfortunately, that the soil thermometer was unreliable when the tempera-

[1] Bog conditions in southern Michigan, which lies toward the southern limit of their distribution in this country, seem to be quite different from bog conditions farther north described by GANONG (**11**). This point was emphasized also by TRANSEAU (**17, 18**). See also BASTIN and DAVIS (**1**).

ture of the air fell near the freezing point, and hence the early spring and late fall data were untrustworthy. In any temperature of the air ranging above 7° C., the records were found to be reliable.

The temperature of the air at First Sister Lake, in the floating sedge zone, compared with that on high ground in Ann Arbor at 7 A.M. is given below.

FIG. 2.—Thermographs in the bog shrub zone at First Sister Lake; the one on the left is recording air, the other soil temperature; photograph by STEELE.

TABLE I

DIFFERENCES IN TEMPERATURE IN BOG AND UPLAND; BOTH RECORDS WERE MADE WITH THERMOGRAPHS

WEEK	HIGHEST		LOWEST	
	Bog	Upland	Bog	Upland
April 26–May 3.....	5° C.	14°.7 C.	−1° C.	2°.4 C.
May 3–May 10.....	7	10.1	4	0
May 10–May 17.....	11	18	−1	0
May 17–May 24.....	10	14.2	−2	3.6

Table I shows that in the morning the temperature of the air in the bog is several degrees lower than that of the upland. The only exception in a much larger collection of data than published

here was seen in the lowest point reached during the second week when the upland went to 0, while the bog remained 4° warmer.

The records of the thermographs show wide variations in air temperatures. In 1907, during the week April 26–May 3, it ran from 21°.5 C. to −4°.5 C.; in 12 hours it rose from −4°.5 C. to 16° C.; May 11, from 6 A.M. to 8 A.M., the air was −4° C.; May 13 at 1 P.M. it reached 28° C.; May 16 at 3 A.M. it was only 1°.5 C. Low temperatures were recorded during the summer. On June 28 the air got as low as 4° C. July (1907) was the hottest month, judged from the lowest temperatures reached, the lowest for the month being 7° C. at 6:15 A.M. the 27th. In August the low records were: the 1st, 9° C.; 3d, 6° C.; 4th, 6° C.; 13th, 7° C.; 22d, 3°.5 C.; 25th, 5° C. August 6, 1904, a maximum-minimum thermometer was hung in the top of an 8-foot tamarack in the sedge zone at Dead Lake. It showed a maximum of 37°.8 C. and a minimum of 5°.5 C.

These figures show that the temperature of the air is comparatively low during the entire summer during the night. The coldest time came at 1 A.M. or about 7 A.M. On the other hand, day temperatures may run very high. The hottest time of the day was about 1 P.M.; it seldom came as late as 2 P.M. Fig. 3 reproduces the air record for the week July 2–9, 1906, taken in the floating sedge zone at First Sister Lake.

The temperature of the soil, on the other hand, shows very slow variations during the season. There is great difference in soil temperatures at different depths, and they warm up very slowly, except for the shallow surface layer; they never get very cold. When making contour maps of the bottom of these lakes (**3, 4**) in winter, it was soon learned that although the ice might be 10 inches (25.3 cm.) thick over open areas, a good thrust of the drill would usually send it through the thin ice near and beneath the tamaracks. Even in most severe weather it was necessary to wear rubber boots, as the thin ice continually broke under one's weight. What ice is formed, however, lasts long into the spring.

In taking soil temperatures, a square piece was sawed out of the peat and carefully removed. The long bulb of the thermo-

graph was then inserted in the side of the opening parallel to the surface for about 18 inches (45.8 cm.), and the piece of peat was replaced. The surface arrangement was left as nearly normal as possible. Some of the records were made at Dead Lake, but most of them were made at First Sister Lake.

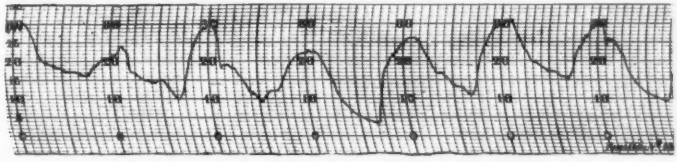

FIG. 3.—Temperature record of the air for the week July 2–9, 1906, taken in the sedge zone at First Sister Lake; the highest was 31° C., the lowest 3°.5 C.; this occurred about 5 A.M., July 6.

Fig. 4 shows a partial record of the results which were obtained at the latter lake at different depths in the tamarack zone. *A* is taken from the figures of TRANSEAU (**18,** p. 421) and gives the readings at a depth of 1 inch (25 mm.). At this depth the rise in temperature is quite rapid and resembles that of the adjacent uplands. At the time the leaves began to appear, May 27, it had reached 17° C. Line *B* gives the record for a depth of 4 inches

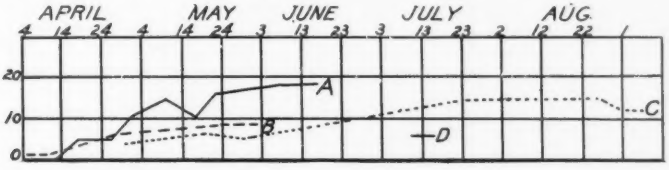

FIG. 4.—Diagram showing variation in temperature at different depths and at different seasons in the tamarack zone; *A*, 25 mm.; *B*, 10.2 cm.; *C*, 20.4 cm.; *D*, 45.8 cm. below the surface.

(10.2 cm.) to June 1. The temperature at this point does not rise so rapidly as that just given, and on May 25 had reached 9° C. The dotted line *C* gives the temperature at 8 inches (20.4 cm.). This record shows that during the spring, when leaves are unfolding, the soil temperature at this depth remains comparatively low; not until July 22 did it reach 14° C. This was held for about a month (July 22–August 24), when it gradually began

to lower. The readings given in line *D* were taken 18 inches (45.8 cm.) below the surface, and were continued for only a short time; the temperature was surprisingly low.

The next figure (fig. 5) was furnished by Mr. HAROLD STEELE, and gives the results of short readings in several zones. These readings were made in 1904 at the same lake. The soil readings

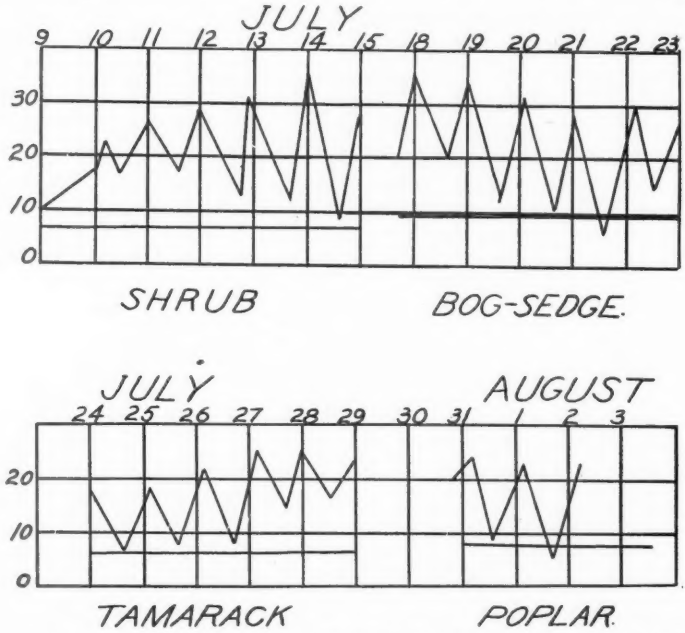

FIG. 5.—Temperature reading taken in different zones at First Sister Lake by STEELE, in summer of 1904; explanation in text.

are taken 18 inches (45.8 cm.) below the surface. This shows that the soil under the tamaracks is the coldest. The same is reported by TRANSEAU (**18**). As the writer had only one set of thermographs at his command, the readings could not be made simultaneously, but the data gathered seem to show that this made little difference in this case, as the temperatures were stationary. The soil temperatures were: tamarack, 6° C.; bog shrub, 7°.5 C.; poplar, 7°.5 C.; and bog shrub, 10° C. These

temperatures for the last two were lower than the author obtained for these zones. As has been pointed out, there is great variation in the poplar zone, and one should have a better knowledge of the exact location before attempting to explain this difference. The temperature under the bog sedge also varies with the width of the floating bog and the proximity to the zone of bog shrubs. That is, the temperature remains more constant when one gets away from the open water.

Average records made by a class with ordinary thermometers for six weeks in the summer of 1906, 3 inches (7.6 cm.) below the surface, were as follows: open water, 18° C.; bog sedge, 17° C.; tamarack, 15° C.; maple-poplar, 17° C.; marginal willows, 18° C.; outer edge of marginal zone with no shade at 1:15 P.M., 22° C.

These readings show a wide divergence of soil temperatures in the zones under consideration, and also at different depths in the same zone. This calls for a study of the depth of the root systems. For example, the high temperature of the soil at 25 mm. represents the condition for germination of the many seeds of "drained swamp" plants which yearly lodge in the bog. This taken with the weak light and humid air, which will be considered later, makes an excellent place for germination of these seeds. On the other hand, the study of the root system shows that temperatures found at a depth of 45.8 cm. in the bog sedge and tamarack zones, especially, could not have a direct influence on the plants growing above, as they did not root in that layer but only in the surface layers. This is true even of the largest trees. Added to this fact is the additional consideration that peat is a very poor conductor of heat. The soil readings in these zones which are of the greatest importance are those taken near the surface in a study of reproduction, and those at moderate depths in the study of the present flora.

These data become ecologically important in the light of the work of TRANSEAU (**18,** p. 22), who has shown by experiment that a temperature of 10°8 C. causes a diminution in the development of both roots and leaves. Although the trees began to open their buds the last of May, it was not until July that the temperature about the roots of the tamaracks reached a higher temperature.

This was after the most active vegetative period. Conditions in the bog shrub zone closely resemble those just described. In bog sedge the records show less regularity and resemble more closely swamp conditions, especially, as has been said before, in bogs where this zone is narrow.

In the two outer zones, the temperatures recorded resemble more closely the upland and drained swamp conditions. Here they ranged about 18° C., in July reaching this mark early in the summer. They would have a less detrimental effect upon the root systems of the plants in these zones.

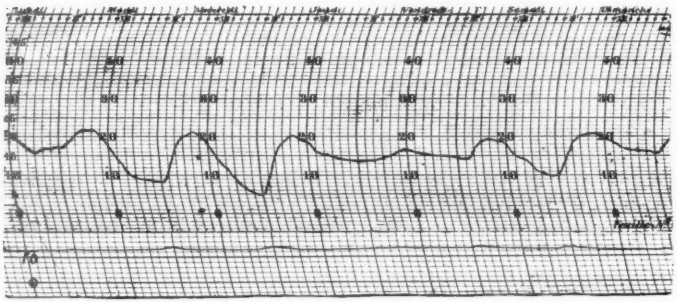

FIG. 6.—Record of soil and air temperatures made at First Sister Lake, Ann Arbor, Mich., August 23–30, 1907; the instruments were in the bog sedge zone; the bulb of the soil thermograph was 20.4 cm. below the surface; the upper line shows record of the air, the lower the soil thermograph.

Fig. 5 also shows the range of air temperatures for the periods given above. The results are similar to those already given by the author.

The record of the soil and air thermographs for one week, August 23 to August 30, is reproduced in fig. 6. This is only one of numerous records which were taken, and shows the very slight variations in the temperature of the soil and the great variations in the temperature of the air. The greatest variation in soil was about 1° C.; that of the air was 17° C. In fig. 3, the variation in air temperature was 25°5 C.

Water table

The variations in the position of the water table from year to year and from month to month play a very important part in the succession of plant societies in these bogs. In 1908 the level of the water in all bogs of southern Michigan was high. In 1901–1904, when the maps of Dead Lake were made (**3**), there was an island near the center, and it was customary to row out there and leave the supplies when working at the lake. That island in 1908 was submerged, and one could row over it in 18 inches (45.8 cm.) of water. The flora of upland forms had disappeared with the exception of some stunted willows, and in its place were a few potamogetons, chiefly *P. heterophyllus*. At Whitmore Lake, north of Ann Arbor, the same rise in water has occurred, and what was a peninsula in 1904 is now an island. The same fact is recorded by DAVIS (**9**, p. 162).

During a series of wet years the change in water level affects the vegetation in all zones except perhaps on the lakeward side of the floating sedge, which rises and falls with every change of level. Along shallow shores the factor is sufficient to control the character of the vegetation, as has been pointed out in the case of the island at Dead Lake. Its influence is also profound in those zones where the peat is solid. It may rise above the surface to a depth of several inches. With this rise there is also found an increase in the humidity of the air. During such periods *Sphagnum* sp. spreads rapidly toward the shore and may assume quite an important position in all zones except perhaps the marginal. An interesting example of the behavior of this moss during wet and dry periods is found at Mud Lake. Here a section was made which showed alternating layers of *Sphagnum* and *Polytrichum* corresponding to the wet and dry periods of previous years. As many as four layers were easily distinguished at Mud Lake.

In one case measured the shrubs stood in water which was 18 inches (45.8 cm.) deep one summer, and in water of various depths less than that for a period of at least three years. These plants then must be able to endure submergence for a long period, as has been pointed out by DAVIS.

During wet periods bog plants show a tendency to move shoreward. This is due to local conditions rather than to historic factors. Such movement is only temporary.

In the summer of 1909 the island in the center of Dead Lake had begun to reappear. During the late summer the ground appeared in the higher parts, showing that the water level was getting lower. In less than ten years the island disappeared and in part reappeared, which indicates that these wet and dry periods may be of short duration. This is contrary to the belief, often expressed, that in southern Michigan they last about thirty years each.

The effect of the dry periods upon vegetation is also very marked. The relation of such periods to plant succession has been emphasized by DAVIS, who believes that they offer an explanation of the xerophytic structures of bog plants (**9**, p. 160). During such periods the surface layers of the peat become exceedingly dry; this may extend to a depth of several feet. Fires which reduce the surface several feet are of common occurrence. The effect of fires upon plant succession has been given by PENNINGTON (**13**).

During this time there is very little water available in these surface layers for plants, and, as it will be shown later that the movement of water in peat is slow, it can easily be seen that the habitat is very dry, even omitting the usual factors of humus acid, low temperature, bog toxins, etc. The following table is given by DAVIS taken from WARRINGTON (**19**).

TABLE II

PARTS OF WATER PER 100 PARTS OF DRY SOIL

Type of soil	When plants wilted	Absorbed from moist air
Coarse sandy	1.5	1.15
Sandy garden	4.6	3.00
Fine humus sand	6.2	3.98
Sandy loam	7.8	5.74
Calcareous	9.8	5.20
Peat	49.7	42.30

DAVIS says: "If these results are correctly reported, it appears that peat may appear very wet and yet contain no water for plants growing in it, so that

those plants which habitually grow at levels of peat bogs, where the surface strata can dry out, must have xerophytic adaptations if the climate is such that drying out of these levels may occur."

In addition to the variation in water level due to wet and dry periods, there is the variation from month to month during each year. This difference is shown in fig. 7, which gives the results obtained April 20–August 3, 1905, in the zones at First Sister Lake. The data were gathered for the most part by STEELE. Holes were

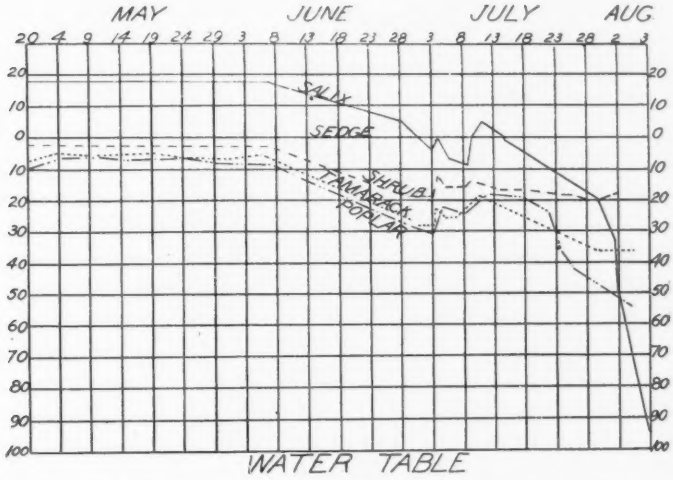

FIG. 7.—The results of measurements taken to determine the variations in water table in the different zones at First Sister Lake; variations are given in cm.

dug in the peat of the different zones to a considerable depth, and a stick placed in a horizontal position at the top. From this stick measurements were taken daily to the top of the water standing in the holes. These were plotted and the result shows in the figure just given.

The bog sedge zone shows practically no variation, although there would have been some, especially on the landward side, had the measurements been started very early in the spring. This however would be too early to affect the vegetation. The open water shows some variation in the summer, but the bog

sedge rises and falls with it, and there is little variation during the growing season.

The other zones show a gradual lowering of the water table, beginning quite rapidly June 8 and continuing until July 3. At this time a heavy rain fell, raising the water level sharply in all zones. After this there was a rapid lowering of its position in all zones until the close of measurements, except in the bog shrub; this showed a slight rise.

The greatest variation, as has been said, was in the marginal zone. On April 20 the water was 7.2 inches (18 cm.) above the surface of the peat. This gradually lowered until the water table was 38.4 inches (96 cm.) below the surface. A variation of 45.6 inches (113 cm.) was recorded.[2] In the maple-poplar zone the variation was 18.4 inches (46 cm.); in the tamarack zone, 12.4 inches (31 cm.); in the bog shrub zone, 6.8 inches (17 cm.). These figures show that the loose peat acts as a dam, holding the open water in the lake from flowing back to the outer zones. The same fact was reported by a former student (**14**) at the small bog near Carpenter's Corner. Here a central area was found with the characteristic bog flora of this region, while the greater part of the original lake was occupied by a mixed flora, with red maple and poplar as the dominant trees. This seemed to be an example of the "lagging behind of a xerophytic group of plants in a hydrophytic habitat," but borings showed that the water table was only 1.4 inches (6 cm.) from the surface. The temperature of the soil and character of the peat were the same as generally found under such plants. A few rods to the east, under the maples, the water table was several feet below the surface.

An excellent example of the holding back by peat of the water in a lake was related to me by a former student, after he had examined the above chart. A farmer living near his home had a peat bog with a very wide marginal zone and a low shore of considerable width. During dry years he was able to cultivate this ground with good returns, but during wet years he always lost his crop. Accordingly, in order to secure continuous use of his

[2] In the report in Science N.S. **29**: 269, the height of the water above the surface should have been added, making a total of 113 cm.

land, he dug a ditch from the margin to the open water during the dry season of 1903. As soon as his ditch was opened, the water flowed from the open lake to the margin and he lost the use of the land entirely.

These examples show that there is very little movement of water in peat. The water may be several feet higher in one zone than in an adjacent one; the difference in height depends upon the nature of the peat. This fact is well known to persons traveling on northern bog areas.

The variations here shown to occur in the position of the water table in different zones during the summer and in the same zone during the season, bring very strong additional proof to the statements of DAVIS regarding the xerophytic structures of bog plants, which were quoted above in the discussion of bogs during a dry period of years. During the season the plants growing in these bogs are subjected to high water level in the spring, when the water table in all zones is approximately level with the open water of the lake. During the hottest and driest months of the summer the water supply is greatly reduced by a lowering of the water table, and when water is removed by the surface layers, it is very slowly replaced by that of the deeper parts. It is only in these surface layers that these plants root. In any bog where a clearing of any extent has been made, one finds areas where the tamaracks have been blown over during storms; these show that even the largest trees root in the surface layers only.

It has been shown in fig. 7 that the water table in the various parts of the bog stood at different heights during the summer. This is the controlling factor which makes the bogs in this region heterogeneous habitats, supporting xerophytes in three zones and hydrophytes or mesophytes in other zones.

The first effect of lowering the water table, as has been pointed out, is to make the habitat xerophytic, and one would expect that those areas where the water table is lowest would be most xerophytic. A glance at the plants shows that this is not the case; the outer zone in this lake is occupied by hydrophytes. This is due to secondary changes. Immediately after the water lowers, a number of other changes set in which produce the opposite

effect. With the decrease in the position of the water table, there is an increase in the oxygen supply, the number of soil organisms, and a rise in temperature. These produce a change in the composition of the peat, making water more and more available for plants and making the habitat less and less xerophytic. In older parts where this process has been going on for years, there is a decrease in the volume of the peat and a lowering of the surface. In the areas studied around Ann Arbor, this seems to be the explana-

FIG. 8.—Station under the tamaracks, showing *Chamaedaphne* almost entirely dead; the light value here was 0.033; photograph by STEELE.

tion of the marginal ditch characteristic of bogs there. In other areas different reasons have been given, but they do not seem to explain the condition found in this region (**16**). During wet periods the width of this ditch is often greatly increased, as has been pointed out previously. In such an area only those plants can grow which can stand high water during a term of wet years and high water during the spring of every year. The vegetation which is found here is much the same as that found under these conditions along the borders of our streams. The peat found

below the lowest level to which the water table gets in the driest times is red, while that above varies from red to brown and black. As has been pointed out, plants do not root in the red peat.

Humidity

Only a few readings were taken with some evaporimeters belonging to the Carnegie Institution and loaned by LIVINGSTON. The total evaporation for seven weeks was as follows: under tamaracks in sphagnum, 275 cc.; on floating sedge, 321.7 cc.; in an adjacent oak-hickory grove, 860 cc.; in an open field bordering the lake, 1056 cc. The last figure is short two days because the instrument was broken. These data, however, give conditions only near the surface, and are of value only in a study of germination in the different zones. It has been pointed out recently (**21**) that great variations are found in short distances above the surface in the amount of water lost by evaporimeters. A lack of instruments made it impossible to study this phase of the subject.

Light

Light readings were made with the usual form of photometer. It was found that the light falling upon the tallest plants in all zones was approximately the same. Great differences were found between these values and those light values found at the surface in the different zones. With light value in the open as 1, the following values were found: under *Chamaedaphne*, 0.0026; under tamaracks, 0.033; under brambles found in a clearing society where maple and cherry seedlings were found in large numbers and some few individuals of each had reached a height equal to the brambles, the light was only 0.00022; among the leaves of the brambles it was 0.166. The value 0.033 seems to be the minimum light requirement for *Chamaedaphne* in the region about Ann Arbor. Fig. 8 shows dead *Chamaedaphne* at First Sister Lake where the light value was 0.033.

The data recorded above show that the bogs of southern Michigan are for the most part not xerophytic habitats, but by far the largest areas are either hydrophytic or mesophytic. Only two or perhaps three of the zones can be considered as xerophytic habitats;

the two are bog shrub and tamarack. To these might be added, depending upon its width chiefly, the bog sedge. This conclusion is justified both by a study of the vegetation and the physical conditions. It is believed that the data furnished at least point strongly toward the supposition that these zones are today xerophytic habitats, even though they also prove that these same areas cannot long remain so. Numerous attempts have been made to explain the xerophytic structures in the plants found in these zones, but only slight reference need be made to them in this paper.

Some have regarded the peat bog as a hydrophytic habitat. Thus WHITFORD, after adding to other factors that of "insufficient aeration of the soil which prevents a healthy growth of the root system of land plants and also bars the presence of nitrifying bacteria," says that "these probably bring about xerophytic structures of plants so commonly seen in hydrophytic habitats." He quite correctly regarded the bog chiefly as a hydrophytic habitat. In the area in which he worked also the true bog plants were not as limited in their distribution as in southern Michigan. It is quite probable that other conditions would enter into a detailed study of bogs in the northern part of the state (**20**).

CLEMENTS (**6**) feels "that the current explanation of xerophytic bog plants, etc., is probably wrong, and that the discrepancy between the nature of the habitat and the structure of the plant is to be explained by the persistence of a fixed ancestral type."

SCHIMPER (**15**) attributes the xerophytic structures to the presence of humus acids in peat which impede absorption. LIVINGSTON (**12**) has shown that any effect produced by humus acids must be chemical, as "bog waters do not have an appreciable higher concentration of dissolved substances than do the streams and lakes of the same region." NILLSON attributes differences in structure between swamp and bog plants to a difference in food supply, but this will not hold in this area.

TRANSEAU believes from his observations and experiments that "in so far as southern Michigan is concerned (**18**, p. 36), the substratum temperatures prevailing in bog areas do not seem to be adequate to account for the presence or absence of bog plants

or their xerophilous structures. Experiments suggest, however, that farther north this factor is of prime importance"; again, on page 37, "an examination of all physical and chemical data now available fails to account for the differences in the flora of the bog and swamp areas of this region. The most important factor is believed to be the physiographic history. Where the habitat dates back to Pleistocene times and has remained undisturbed, we find today the bog flora. Where the habitat is of recent origin or has been recently disturbed, we find the swamp flora, or a mixture of bog and swamp species."

DACHNOWSKI (**7, 8**) believes from his experimental work that the condition which gives rise to xerophily and to zonation in bog plants "lies rather in the toxicity of the soil substratum, that is, in the production of unfavorable soil conditions brought about by the plants themselves." This author further says that "if water transpired is replaced by bog water," which would be the case to a limited extent during the summer when the water table was low and conditions for transpiration excellent, "the soils become more toxic." That is, the first effect of lowering the water table would tend to make the habitat more xerophytic. Further, "decrease in toxicity always follows aeration of the soil and drainage"; that is, an increased lowering of the water table admits oxygen, decreasing the toxicity of the soil and making the habitat less xerophytic. With this is also associated an addition of humus which increases the capacity of the soil "for the adsorption and retention of the toxins." If the results obtained by DACHNOWSKI are correctly explained by him as due to bog toxins, they do not conflict with the data recorded in this paper. It is to be hoped, however, that his studies will be pushed farther.

DAVIS, as has been pointed out earlier in this paper, believes that the bog is a xerophytic habitat, due to the drying of surface layers and the ability of peat to hold large amounts of water which are not available for the plants. The data given in this paper are in accordance with this view, and it appears to the author to more nearly cover conditions than any of the other theories advanced. It is not contradictory to the experimental work of the authors cited; this has been shown in the case of the work of DACHNOWSKI.

TRANSEAU suggested that in the regions farther north the temperature of the soil may be of prime importance. Temperature readings in deeper layers in the bogs of southern Michigan than those which he discusses, and yet not too deep for the root systems, resemble those of northern areas, and it is probable, in the light of his experiments, that they may be a controlling factor, even in those of southern Michigan.

YAPP (**21**), in his excellent paper dealing with the relation of marsh flora to evaporation, has shown that great variation exists in the amount of water that is evaporated by instruments placed at different heights above the surface. Hence two plants may grow side by side and yet not be under identical conditions. He produces a large amount of data, especially concerning factors affecting the aerial parts of plants. He concludes that "any argument drawn from mere proximity of position, without reference to the varying physiological problems of the different species, is entirely insufficient," and that "the arguments of authors, who insist that the so-called xerophytic structures of marsh plants can have no reference to present-day conditions, because both xerophytic and non-xerophytic species often grow side by side in nature, are entirely inconclusive."

Summary

1. The bogs around Ann Arbor are not xerophytic habitats, as such, but contain xerophytic, hydrophytic, and even mesophytic areas.

2. A study of the conditions in those areas which now are xerophytic indicates clearly that xerophytic conditions in bogs of southern Michigan will shortly disappear.

3. The presence of definite groups of plants in each zone is due chiefly to soil conditions found in that zone; also to position of the water table and secondary changes dependent thereon, as aeration, temperature, composition of the peat, etc.

4. The absence of certain plants from certain zones is due to decrease in the amount of light. *Chamaedaphne* apparently is not able to grow in this area in a light of 0.033.

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THE VEGETATION OF CRANBERRY ISLAND (OHIO) AND ITS RELATIONS TO THE SUBSTRATUM, TEMPERATURE, AND EVAPORATION. II

ALFRED DACHNOWSKI

(WITH ONE FIGURE)

The atmospheric influences as ecological conditions for growth

Various theories have been suggested to account for the presence and the relative persistence of this northern boreal flora under present climatic conditions. Some of these theories have been referred to earlier in the paper. Although widely separated from the central region of active bog formation with which the local bog is now only historically connected, its persistence and existence in spite of the climatic changes and animal and plant migration and invasion since the last glacial period, and the fact also that many peat deposits are reported to occur beyond the margin of the Wisconsin ice sheet, suggest that the most significant ecological factors are not to be looked for in the continuation of limiting conditions similar to those which prevailed when a colder climate existed than at present. That bog plants are related functionally as well as morphologically, and that they are grouped and localized with reference to more or less definite conditions of their environment is now a fact no longer questioned. It is also well known that no formation or plant society is likely to be relatively permanent and stationary, for there are changes constantly taking place in the environment as well as among the dominant plants and their associates. In the bog, however, but few successions of plants are in evidence, and the treatment of the vegetational societies from the standpoint of floristics and succession is therefore relatively free from complications. On the other hand, the determination of the factors in bog habitats, and the more detailed study of the dynamics of the process, that is, how some factors are related, their influence and duration—this phase of the problem is still in a state of uncertainty, and the methods of study have been all but satisfactory. When one con-

siders the bog as a habitat, the various causative and limiting factors entering into the plant environment are not so readily distinguished. In connection, therefore, with the analysis of the life conditions in bogs, associated also with the distribution of bog plants, and their conflict with species whose range is more southern, certain meteorological phenomena have been added below.

CLIMATIC CONDITIONS

One of the main objects kept in view during the progress of the investigation on the ecology of Buckeye Lake, and one which seemed to the writer an indispensable preface to both the field and the laboratory study, has been the climate of the region. The general statistics were taken from *Bulletin Q* of the U.S. Weather Bureau Service (**17**), and from manuscript to which access was had by the courtesy of Section Director HAYS of the Columbus (Ohio) Weather Bureau. No continuous series of climatological records have been made on Cranberry Island. The writer made records extending over the period of investigation; these records were supplemented by Mr. DICKEY, whose readings were taken each time the evaporation of the bog habitat was measured. It is felt that the comparative climate statistics given below are generalized data which do not lend themselves to investigation in physiological ecology. Though facing the same set of climatic factors, few of the species forming the flora of the bog island confront the same physiological problems, and hence any conclusions drawn from mere climatic data, without reference to the varying functional responses of the different species of plants, are certainly inadequate. However, the study of the meteorological observations is suggestive mainly in ascertaining the essential differences between the local region and the conditions found in the northern center of bog formation, and in estimating the average temperature and humidity exposure of the plants. The data given in table IV are for Columbus, Ohio; for Ann Arbor, Michigan, where bogs and swamp-lands are found more abundantly; and for Marquette, Michigan, where this type of vegetation reaches a still higher development.

TABLE IV

GENERAL METEOROLOGICAL CONDITIONS

	Columbus, Ohio	Ann Arbor, Mich.	Marquette, Mich.
Elevation	774 ft.	930 ft.	668 ft.
Years of record	31 yrs.	25 yrs.	33 yrs.
Mean seasonal temperature in degrees F.			
Winter	31	26	19
Spring	51	46	37
Summer	73	70	63
Autumn	54	51	45
Annual mean	52	48	41
Absolute maximum	104	101	108
Absolute minimum	−20	−24	−27
Absolute range	124	125	135
Greatest annual range	118		124
Least annual range	89		97
Frost, aver. date of last in spring	April 16	April 28	May 15
Frost, aver. date of first in autumn	Oct. 16	Oct. 9	Oct. 2
No. of days in growing season	176	157	140
Mean seasonal precipitation in inches			
Winter	8.9	6.6	6.1
Spring	10	7.9	7.3
Summer	10.3	10.1	9.4
Autumn	8	7.6	9.6
Annual mean	37.2	32.2	32.4
Absolute maximum	51.2	47.7	42.9
Absolute minimum	26.4	21.1	25.3
Mean annual relative humidity	79	79	80
No. days precipitation	144	138	161
Aver. direction of prevailing wind	S.W.	S.W.	N.W.
Aver. minimum wind velocity	48 miles	.....	46 miles

From the data in table IV, it will be observed that the seasonal and annual temperature decreases as one travels from the southern limit toward the northern center of bog vegetation. The climate of the region about Columbus is characterized by a milder winter but a relatively hot summer. The annual range in temperature is comparatively smaller than at Marquette, 102° F. as against 112° F. The normal annual range is here only between 96° F. (35°.5 C.) and −6° F. (−21°.11 C.), and the greatest departure from the normal variation does not exceed 16° F. The monthly averages for only two months are at Columbus below 32° F. (0° C.), as against five months for Marquette. The normal number of days per annum with a temperature above 43° F. (6° C.), the factor upon which SCHIMPER (**29**) and MERRIAM (**27**) base the boreal limit, is at Columbus approximately 185, that is about one-half of the year, as against 122 days at Marquette. The

normal sum total of effective daily temperatures above 43° F. (6° C.), the estimate for which is derived by multiplying the mean average monthly minimum temperature of that period by the number of days, is 10414° F. (2520° C.), as against 6466° F. (1422° C.) for Marquette. The normal mean temperature of the six consecutive hottest weeks of the year, effective also in determining the austral limit of species, is 75°. The warmest month is July with an average monthly maximum of 86° F. (30° C.), as contrasted with 77° F. (25°C.) at Marquette. The coldest months are January and February with an average monthly minimum of 22° F. and 23° F. (5° and 5°.5 C.) respectively, as contrasted with 10° F. and 9° F. (12°.5 and 12°.0 C.) respectively for Marquette. The dates of the latest killing frost in spring and the earliest in autumn, although not the exact limits of physiological activity in plants, or the limits of the growing period of most plants, are nevertheless an unquestionably important factor. Six months of the year are normally free from frost about Columbus.

Though the relation between rainfall and the amount of water needed by plants is of great importance in regard to differences in vegetation, the rainfall and its distribution during the seasons, and the number of rainy days, are of greater significance than is the amount of rain. At Columbus precipitation is quite evenly distributed, reaching an optimum of 10.5 inches (26 cm.) during spring and summer, when the vegetative functions of bog plants are more active, with a minimum of 8.5 inches (21 cm.) during the season of low temperature and in the quiescent period of plants. Columbus exceeds the annual precipitation at Marquette by 4.7 inches (11.8 cm.); the average number of days with rainfall during the year, however, is considerably less than in northern Michigan, 144 days as against 161 days. In the north the greater precipitation is in the form of snow. Marquette has over five times more snow than Columbus, 125.7 inches (315 cm.), as contrasted with 23.5 inches (59 cm.) here. In this vicinity the longer growing season of the plants has therefore correspondingly more of the precipitation available. On account of the higher temperature more moisture is needed, and hence the evaporation also is much greater here than at Marquette. Cold air does

not take up so much water as does hot air; consequently the additional amount of water which the atmosphere is capable of taking up to become saturated, that is, the evaporating power of the air, is greater here than at Marquette. The amount of evaporation also depends upon several other factors and conditions; the values of these will be taken into consideration below. Where evaporation is nearly as great as precipitation, the seasonal distribution of rainfall and humidity is a matter of greatest importance, for it is known that scanty rainfall throughout the year, or relative dryness of air and soil during the growing season, favors the development of xerophytic forms in almost any region. The relative humidity of Columbus and vicinity is only slightly less when compared with the north, the percentage of saturation ranging from 79 to 80 respectively. The distribution varies during the year only to a small extent between the month of least and that of greatest normal humidity.

The rate of movement of air currents is, no doubt, of great importance to vegetation, not only because of the direct mechanical effect and the indirect physiological action in increasing the evaporating power of the air, but also because transpiration increases with the velocity of the wind. That wind is an ecological factor of the greatest importance has been emphasized by many authors. KIHLMAN and WARMING regard xerophytic structures in plants as acquired and necessary, on account of strong drying winds in exposed places. Even humid atmosphere when continually renewed leads to strong transpiration, and the danger may be decreased only as protection is provided either through density and height of species, or admixture of a variety of species in a community of plants. The average maximum velocity of wind does not vary greatly between Columbus and Marquette, and hence the influence of wind, though considerable in more exposed places, has apparently little relation to the differences to be accounted for in the character of the local vegetation.

Briefly summarized, the region about Columbus and Buckeye Lake is characterized by a longer growing period with a relatively higher sum total of temperature exposure, a milder winter with normally slight variations, well distributed rainfall, and a relatively

high percentage of atmospheric humidity. The local climate is therefore preeminently a deciduous forest climate. The whole region was in its recent primitive condition densely forested. On the other hand, the marked increase of bog development in area and in variety of species in northern localities seems to be correlated with a decline in extremes of summer temperatures and an increase in relative humidity. The general effect is to produce a balanced functional relation, though limited in range, between the amounts of water absorbed and transpired. This phenomenon associated with bog habitats will be discussed in connection with a further analysis of the life conditions obtained in bogs from the point of view of their physiological aridity.

If we take the above mentioned climatic factors into account in the interpretation of local bog conditions, it will be seen that meteorological data in this region are not such as to produce or account for xerophily or for persistence of bog floras. The climatic changes by which a region varies, if severe and varying between wide diurnal and seasonal changes in temperature, humidity, and light, entail naturally modifications in the functions and in the composition of a flora. The vegetation would be tested to the limits of its power of adjustment and acclimatization, and only the forms which had a greater efficiency of responses and had powers of resistance intensified to a new place-function would take up the habitat to the extent in which survival under the modified conditions would be possible. It has been pointed out above that changes in the flora are now occurring and have occurred during the development of the bog island. Many of the former plants have disappeared and are no longer to be found here, while others have survived, hold tenaciously the area under control, and are still constituents of the present flora. Their preservation in this region would seem to be dependent upon less obvious factors than climate. Functional habitat relations, as well as such ecological life relations as are comprised in association, in ecesis, and succession, need therefore the more detailed investigation. In determining these the first component to be considered is the rôle of low substratum temperature. The temperature of a soil is a phytogeographical factor of great significance, but its weightiest

importance is in its effect upon the functional activities of roots and rhizomes. Recently the temperature of soils and its fluctuations have received considerable attention. The relationship, however, and the general effect upon plant forms and the correlated functioning are nevertheless but little understood. This circumstance is perhaps the more to be regretted, since, broadly speaking, it seems that the relationship to plant life is the more favorable the more dominating the influence of the physical characters of the soil and particularly the relations prevailing in regard to the physiological water content and efficient temperature.

THE RÔLE OF SUBSTRATUM TEMPERATURE IN BOG HABITATS

During the first few months of field work the device chosen for obtaining the substratum temperatures was the "thermophone." The apparatus is based upon the principle that the resistance of an electric conductor changes with its temperature. In obtaining the temperature of peat soils at various depths, the coils were sunk to the required depth, and their leading wires were then connected with the respective binding posts of the indicator box. A buzzing sound in the telephone increases or diminishes according to the position of the pointer while receding from or approaching to a section of the graded dial. Hence the position is soon found where the telephone is silent. This point indicates the temperature of the sunken soil. The instrument is very sensitive, but very inconvenient for obtaining weekly and monthly minimum and maximum temperatures. Later in the season the investigations were planned for a set of thermographs such as MACDOUGAL described (**25**), that would make a continuous record of the temperatures at any desired depth. The lack of sufficient funds and the failure to secure similar instruments made it necessary to resort to a conventional though less graphic method of measuring the temperature exposure of plants. In the field work of 1908, 1909, and at present, mercurial minimum and maximum thermometers were therefore used. The thermometers for the deeper peat strata were fastened to wooden poles and pushed down into the soil to the depth of 5 feet (1.5 m.). They remained in the soil during the period of investigation except for such short

periods of time as were necessary to make a reading. For strata nearer the surface differential and ordinary mercurial thermometers were used, the bulbs of which were pushed down into the peat around the rhizomes of the plants to a depth of one foot (20 cm.) and three inches (7.5 cm.), respectively. The glass stems of the exposed instruments remained shaded from the direct rays of light. The temperatures recorded below, in centigrade, were generally taken on afternoons, usually between 12 and 2 P.M. It should be kept in mind that the maple-alder zone conditions correspond very nearly to those of the tamarack-willow-poplar zone of the northern bogs and swamps, and that a similar relation exists between the local central zone and the open bog-sedge zone of northern bogs.

The readings taken during the period of observation are too voluminous for a tabulated record. Only those of the seasons of 1909 will be given in this place (table V).

TABLE V

TEMPERATURES (C.) IN THE PEAT SUBSTRATUM OF CRANBERRY ISLAND SEASON OF 1909

Station	Jan. 12	Feb. 26	Mar. 29	Apr. 23	May 14	June 11	July 17	Aug. 14	Sept. 11	Oct. 2	Nov. 30	Dec. 28
Central (sphagnum-cranberry) zone:												
Air 1.5 m.	0.5	5	14	23.5	24	26	24	28	27	17.5	14	3.5
Air 30 cm.	0.5	4.5	14	24	25	26	24	28	27	17	14	2.5
Air 7.5 cm.	1.0	4.5	14.5	22	26	29	24.5	28	27.5	17	14	2.5
Soil 7.5 cm.	0.5	1.5	10	12	14.5	21.5	24	25	22.5	16	7	0.5
Soil 30 cm.	0.5	2.0	7	10.5	12	21.0	24	25	22.5	17	8	2.5
Soil 1.5 m.	7.5	6.3	8.5	9	11	16.0	21	22	22.5	21.5	16.5	13.0
Maple-alder zone:												
Soil 7.5 cm.	0.5	1	11	11	16	20	20.5	22	20	14	8	4
Soil 30 m.	1.5	2.0	9.5	10	14	19.5	21	21.5	20	15.5	9	9.5
Soil 1.5 m.	6.5	5.0	8.0	10.5	14	17.5	19.5	21.5	21	19	15.5	14
Lake zone:												
Water 7.5 cm.	1.5	1	13.5	14.5	20.5	26	29	28.5	25	15	6.5	3.5
Water 30 cm.	1.5	0.5	13.5	14.5	20	26	29	28.5	25	15	6.5	4
Water 1.5 m.	1.1	2.7	13	13.8	18.8	22.5	26	26	24	12	6.5	5

A glance at table V shows that the temperature conditions, though comparatively uniform and high throughout the bog island, range somewhat lower in the maple-alder zone than in the central

zone. There is a large daily as well as annual range in temperature, but the range is considerably less in the soil than in the air above. The data obtained are sufficient to strengthen the observation made, that in the spring the ice in the central zone melts with greater rapidity, and that a higher temperature results from the greater insolation and the increased absorption and retention of heat rays. On days following a sudden lowering of the air temperature, and also on cloudy days, the temperature of the surface bog water and bog soil in the sphagnum-covered area stands above that of the maple-alder zone. This gain in temperature is cumulative and aids in the penetration of heat rays below the surface. The heat supply is obviously the most direct factor contributing to the substratum temperature, for the variations are associated directly with the amount and intensity of sunshine. The extreme slowness in the maple-alder zone is explained partly by the low conductivity of the partially decayed peat and the lack of a free circulation of air above the soil, but largely by the increasing diffusion of light rays due to the leafing out of trees and shrubs.

Another point of interest is the fact that notable differences are found between the temperatures of the bog island and the surrounding lake water. When we compare the effects of gain and loss of heat between the free water surface of the lake and that of the peat area clothed with vegetation, it will be seen that the temperature of the central and the maple-alder zone remains higher than that of the lake during the autumn and winter months, and that during spring and summer the lake water is warmer at the respective (1.5 m.) depths than the peat substratum. Water has a specific heat far greater than any soil; it retains its heat longer and for this reason is warmer than the peat substratum in spring and summer. On the other hand, peat and humus are cooled more rapidly at the surface by the evaporation of water during the warm days of the seasons. The values of both heat conductivity and diffusion are in general lower in peat than in water, and hence a rapid loss of temperature in the peat strata below the surface vegetation is thus prevented.

A high temperature phenomenon existing in certain places is worthy of special mention. Not infrequently small sheltered

areas are found in the central zone bordering the *Rhus-Alnus* thickets where ice never forms in winter. Such temperature conditions would not attract special attention were it not for the fact that usually the temperature is so much lower in the adjacent areas. From a biological standpoint this fact is significant because these conditions favor isolation of habitats and produce a prominent floristic difference. *Wolfiella floridana* commonly occurs in these "warm" pools.

Plants are not dependent so much upon the mean annual temperatures as upon the minima and maxima of temperature encountered, and upon the duration of the vegetation season. To throw some light on the characteristic temperature range occurring throughout the year and within a growing season, the temperature data of the monthly extremes for the seasons of 1908, 1909, and for the autumn and winter of 1907, and the spring of 1910 are appended. As far as the writer is aware, no observations of minima and maxima temperature records within a bog, covering a period of three years, have been carried out thus far. On account of the fact that the present data were obtained at a station whose ecological significance is especially interesting, table VI of the temperature data is deemed worthy of a closer consideration.

We see again that the temperature of the substrata at the different levels is affected less by the alternate heating and cooling at the surface, but in a far greater degree by the progression of the seasons. It increases slowly during May, is stationary more or less during August and September, and begins to decrease fairly rapidly in November. The maximum temperature occurs in July and August, and the minimum temperature is registered in January for the central zone. That of the maple-alder zone occurs in February. Observations have shown that the lake freezes to a depth of 8–15 inches (20–37 cm.), while the bog is covered by ice to a thickness varying from 3 to 5 inches (7.5–12.5 cm.), except for a few places where ice never forms. Consequently, the strata in the bog area below the one-foot level (30 cm.) are well protected from lower temperatures and from sudden temperature changes. When the sun's heat melts the ice and snow, the percolating water derived from the melting ice lowers the temperature of the deeper

strata a few degrees in the early spring. The wave of temperature increase falls here slightly behind in March, but the upper strata are not prevented from rising in the meanwhile rapidly above the freezing point. Though of ecological importance as a protective cover during the winter months, and of significance as a bad conductor of heat and in decreasing fluctuations in temperature, the ice and snow do not, therefore, retard appreciably the beginning of favorable growth conditions. The maples and willows of the

TABLE VI

MINIMUM AND MAXIMUM TEMPERATURES IN THE CENTRAL ZONE AT CRANBERRY ISLAND, 1907 to 1910

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Air:												
Max.....	18.3	15	25	27.2	31.6	33.3	35	35	34.5	30	23.3	19
Min.....	−19.4	−24.5	−8.8	−7.7	0.5	3.3	8.3	7.2	−1.6	−5.5	−9.4	−21.6
Range....	37.7	39.5	33.8	34.9	31.1	30.0	26.7	27.8	36.1	35.5	32.7	40.6
Soil: 1 ft.(0.3 m.)												
Max.....	4.5	3.3	9	13.3	15	25	27	25.5	25	17.7	13	9
Min.....	0	1.2	0	6.6	10	18	17	21.	16	12.5	8	2.5
Range....	4.5	2.1	9	6.7	5	7	10	4.5	9	5.2	5	6.5
Soil: 5 ft.(1.5 m.)												
Max.....	13.3	9.2	9	12.2	12.5	17	23	26	22.5	22	20	15.5
Min.....	7.5	3.9	4	7.2	9.5	14	16	22	20	18	16.5	13
Range....	5.8	5.3	5	5	3	3	7	4	2.5	4	3.5	2.5

GREATEST RANGE

Air: max. 35; min. −24.5; range 59.5.
Soil 1 ft. (0.3 m.): max. 27; min. 0; range 27.
Soil 5 ft. (1.5 m.): max. 26; min. 3.9; range 22.1.

bog island are in flower about 8 to 10 days later than those on the campus of the university. A persistence, however, in the peat substratum of the winter cold and ice through the summer months is not proved, at least in this region. The records taken at a depth of 5 feet (1.5 m.) below the surface vegetation show a variation in temperature between 3°.9 C. and 26° C., i.e., an annual range within 22° C. At this depth only the anaerobic bacterial bog flora is most active. The roots and rhizomes of bog plants do not penetrate beyond the depth of 2 feet (0.6 m.), and the roots of

maples still less. Plants imbedded in the peat at a depth of 1 foot (0.3 m.) are within ranges of temperature from 0° C. to 27° C. The underground growth of the plants continues when the winter temperature in the substratum rises and reaches the gradient from 4° to 8° C. When these soil temperatures prevail during winter for a sufficient length of time, the different stems and buds shoot upward and develop leaves and lengthen their internodes rapidly in the warmer weather of spring. The absorbing organs at 3 inches (7.5 cm.) depth in the peat substratum encounter a mean average of 13°.5 C. with an amplitude of more than 30°. In all cases, however, the range of temperature in the maple-alder zone is less than that of the central zone by a difference of at least 6°.

These observations and facts disclosed as to the actual temperatures in the peat substratum of Cranberry Island, and the seasonal changes therein point to the following conclusions:

1. The soil temperature of two plant associations formed about the bog island are slightly different, and each association has its own characteristic temperature range.

2. Of the two plant associations in the bog area, the one more liable to extreme low temperatures in the spring and during the growing season is the maple-alder zone along the border of the lake, and not the more xerophytic central zone.

3. The substratum temperatures as phenomena of the local peat deposits are not favorable to the preservation of bog types, if low temperature is considered to be an edaphic criterion; in connection, therefore, with an analysis of the life conditions in this bog area low temperature is not a limiting factor.

4. A persistence of the winter cold and ice through the summer months is a point not proved either by observation or by registering instruments. The persistence of northern forms in this bog, therefore, has some other cause than low temperature of the substratum. In arctic latitudes, no doubt the most significant factor in determining the character and the distribution of plants, as well as in the formation and preservation of humus material, is low temperature. In the latitudes of Ohio, temperature is not a factor in the process. Neither does the accumulation of humus finally bring about edaphic conditions "too cold and too acid."

5. It is not low temperature that kills invading mesophytes, but the edaphic physiological aridity prevailing in the central zone, which decreases the absorption of water by roots at a time when transpiration and the growth of the plants demand a greater physiological soil-water content.

6. The topographical distribution of plants in the bog is also affected by relations in regard not to low temperatures, but to the uneven physiological water content and the physical condition in the peat substratum.

THE DIFFERENCES BETWEEN AIR AND SOIL TEMPERATURES

We proceed now to a brief consideration of the question whether the differences between air temperature and that of the soil are sufficiently marked during the growing period to prove a factor in the selection of plants for bog areas. To show this relation, data on the corresponding minimum and maximum air temperatures for the period under investigation have been added to table VI. The records were taken from the Climatological Service of the U.S. Weather Bureau at Pataskala, some 35 miles (0.56 km.) distant from Buckeye Lake. They represent fairly nearly the conditions at Cranberry Island on the corresponding period. Additional data are found also in table VIII. Upon comparison it will be seen that during July and August, the months which proved most critical for the cultivated plants grown in the bog area for experimental purposes, the shoots of plants were in an atmosphere varying between 7° and 35° C., while the roots and rhizomes were at temperatures varying between 16° and 27° C., i.e., within a range of temperature differences not less than 9° and not more than 19° C. For a growing season lasting from May 5 to October 1, the average date of the latest and earliest killing frost, the actual differences between the temperature of shoots and roots amounted to 34°.5 and 21° C. for each of the absorbing and transpiring organs respectively in the central zone, i.e., within a range of 29° C. It is seen that rapid and passing changes of air temperatures and the occasional extremes do not affect the substratum temperatures. Only average effects prevail and the

great periodic seasonal changes. In winter and in summer the minimum temperature of the peat substratum is considerably higher than that of the air. Consequently, the annual mean temperature of the soil greatly exceeds that of the air. The monthly and annual fluctuations of temperature affect the peat area to a depth of 2 m., but they are at no time greater or with a wider range than those of the air. At what depth the mean temperature would remain constant has not been determined.

That the differences between the temperatures of the air and that of the substratum are not as great as is generally supposed, is a fact upon which it is needless to elaborate further. They cannot be looked upon as factors in bog development or in the characteristic xerophily of the sphagnum-covered area in this region, and hence neither the substratum temperature nor the differences between soil and air temperature are of sufficient importance to enter into the problem of bog flora, and zonation or ecesis and succession. The records show that on the basis of temperature as the initial factor the central zone conditions are somewhat more rigorous, and that these conditions are mitigated in the maple-alder zone; but it cannot be claimed that the differences of the plant covering in the two zones are directly correlated with the differences of temperature. With no attempt to minimize its influence, it is evident that for a comparison of habitats, temperature, at least as a single physical factor, is a matter of very subordinate importance on which to establish a causal relation. Those factors acting in conjunction with it demand the greater emphasis. It is questioned, therefore, even for regions where bogs reach their optimum development, whether the coefficient of the differences between the soil and air temperatures is to be looked upon as having a greater value than here in the selection of plants for bog areas, or the production of xerophilous characters.

Whether or not important correlations between the temperature differences and the transpiratory activities of bog and other plants may be expected, a study of the transpiration quantities will doubtless reveal. Work of this character is now in progress and will be published as soon as opportunity permits.

THE RÔLE OF THE EVAPORATING POWER OF AIR

As a preliminary study to the transpiration value of bog plants and to the question also whether the xerophytism and the stunted growth so manifest on maples, poison sumach, and various other plants in the central zone is brought about by an excessive evaporating power of the air, quantitative measurements have been made by the volumetric method to determine the saturation deficiency of the air in three representative stations.

Evaporation is one of the most important factors of the meteorological cycle of a locality. To the student of agriculture and of plant physiology it is a problem the study of which aids in supplying much of the desired information on the growth of plants in irrigated and uncultivated fields. HANN (**16**), who studied evaporation chiefly from the point of view of the meteorologist, has pointed out that the amount of water which the atmosphere is capable of taking up to become saturated is one of the indices of the influence of climate. The highly important observations made by LIVINGSTON (**21, 23**) emphasize the fact that the effect of an atmosphere of great evaporating power undoubtedly influences the geographical distribution of plants, and through its local variations exerts an equally determining effect as a physiological and an ecological factor. The problem of evaporation has been but imperfectly appreciated, and though the bibliography of evaporation is extensive (**24**), the correlation between the evaporation under different conditions has not been satisfactorily formulated. The evaporating power of the air is generally understood to comprise a resultant of temperature, humidity, and wind. But evaporation is very sensitive to soil as well as to air relations, and since a multitude of local factors may influence either of the two conditions, the amount of evaporation integrates the effect of numerous variables. Evaporation is a rather complex resultant, therefore, and in preparing for an investigation which has in view the measurement of the amount of evaporation in plant societies, it is important to keep in mind the several conditions entering into the problem. It is necessary to recognize that the essential details of the phenomenon of evaporation are different in the great variety of conditions, and require separate and special study

appropriate to the peculiar conditions. To measure evaporation in a few places in this locality, and then to assign the results to the region as a whole, is a procedure not without its accompanying shortcomings. It was intended to overcome this difficulty partially by measuring the variation in evaporation of the vertical as well as the horizontal vapor pressure gradient in a larger number of stations, plotting the results, and drawing isothymes. By a summation of the evaporation, that of the whole area could be calculated with greater accuracy. The distance of Buckeye Lake from Columbus and the inconveniences as to available time have made it difficult to secure the required observations. However, the problem here dealt with does not concern itself with the development of a formulated expression of evaporation for this region. The purpose at present is to obtain quantitative data on the rate of evaporation, and thus to secure direct evidence as to the relation of the observed evaporating power of the air and the nature of the vegetation. The more detailed study of the phenomenon as originally outlined is now in progress.

The ordinary markets are not prepared to supply the well designed standardized self-registering instruments which have been devised to meet the needs of the Weather Bureau (**26**). For ecological purposes, an instrument is required which can be placed under conditions practically identical with those which the plants themselves endure. For this purpose a small atmometer partly buried in the soil is desirable. Dr. FORREST SHREVE of the Carnegie Desert Laboratory, Tucson, Arizona, courteously left at the disposal of the writer several porous cups of the type as described and used by LIVINGSTON (**21**). The instruments had been previously standardized with an atmometer at Tucson, and since they are similar to those sent out from the Desert Laboratory to various other stations in the United States, the readings obtained may be readily compared. There are certain objections to the porous cups as an instrument in the field study of habitat conditions. The inability of the cup to withstand frost makes it practically impossible to obtain readings for more than the growing period of seven months, and the fact that the instrument does not prevent the direct entrance of rain to the jar

introduces an error which becomes very large as the time interval between the reading of the instruments and the length of time and the amount of precipitation increases. The instrument recently described by YAPP (**34**) and by LIVINGSTON eliminates the error last mentioned, but some weighing method, when available, will probably be more exact than any, since it alone can be employed in the measurement of evaporation from ice, snow, and growing vegetation.

Of the instruments on hand, one was established as a standard in an open lawn freely exposed to the sun and wind on the campus near the University Observatory. It was placed in a manner to obtain readings on the saturation deficiency of the air at a height of 15 cm. above the soil surface. The atmometer remained in the care of Professor H. C. LORD and his assistant Mr. KENDRIG, to whom the writer expresses his warmest thanks for their helpful interest. The records were taken three times daily in connection with the climatological observations called for by the U.S. Weather Bureau Service, and consisted of the reading of the depth of water remaining in a graduated container. The instrument continued in operation from May 21 to September 17, when an accident resulted in the breaking of the graduated retainer. Within a few days the trouble had been remedied and the observations proceeded until October 11, when the first heavy frost occurred.

Another cup was placed in an open and exposed place in the cranberry-sphagnum (central) zone, under conditions similar to those of the standard instrument. It was installed May 14. With the exception of the period from June 11 to July 17, when the total for five weeks was recorded, the loss of water by evaporation was determined at intervals of one week by running in distilled water from a graduate, thus restoring the original water level of the container. Records were obtained until August 21, when it was found that the atmometer had been disturbed. A week later it had disappeared entirely. No attempt was made to replace it by another.

The third instrument stood in the shaded conditions of the maple-alder zone. It was placed near large-sized maples whose cover was relatively dense though open. The reading of this

instrument extended uninterruptedly to October 2. During the writer's absence in Europe, the readings in the two plant zones were recorded by Mr. DICKEY; they have since appeared in published form (**12**). It is not necessary to reproduce in detail the original observations for the entire period. A series of data from the observations made have been summarized here and the conclusions stated.

Following are the atmometer readings for the several habitats, together with the comparative evaporation expressed in percentage of the standard instrument (table VII).

TABLE VII

ATMOMETER READINGS FOR STATIONS ON CRANBERRY ISLAND AND THE UNIVERSITY CAMPUS

1909 week ending	University station	Central, sphagnum-cranberry zone	Percent. diff.	Maple-alder zone	Percent. diff.
May 28	118.8 cc.	97 cc.	81.6	78.1 cc.	65.7
June 4	110.9	92.1	83	60.5	54.5
June 11	88.1	53.3	60.5	27.5	31.2
Five weeks ending July 17	487	349.2	71.7	290.4	59.6
Week ending July 24	151.4	120.2	79.3	77	50
July 31	117.8	69.8	59.2	50.6	42.9
Aug. 7	140.6	69.8	49.6	36.3	25.8
Aug. 14	134.6	82.4	61.2	70.4	52.3
Total evaporation	1349.2	933.8	69.2	690.8	51.2

As was to be expected, by far the smaller part of the total evaporation on Cranberry Island occurred in the maple-alder zone. The annual evaporation within the maple-alder zone is now about three-fourths of that in the open central zone, that is, fully 25 per cent of the moisture is saved by shade-producing trees and shrubs. The evaporation within this zone is greatest in the season from October to May. The difference in evaporation between this zone and the central zone is then at a minimum, but later it follows closely the growth of the leaves in the early spring and their fall in autumn. The maximum difference occurs in June and July. As the seasons advance, the evaporating power of the air in the forested zone varies with precipitation. Wind

and temperature are less effective, for as the leafing out of the trees proceeds, and the increased undergrowth also becomes effective in shade and interference with air currents, the retention of the moisture in the air decreases the evaporation rate and the relative humidity is raised. It would be instructive to follow in more detail the effect of the various meteorological factors on evaporation. This effect can very well be seen if the more important factors like temperature, intensity and duration of light, precipitation, wind, soil, and vegetation are referred to individually. But the results are uncertain and suggest the desirability of preliminary investigations in artificially maintained conditions by laboratory methods. In a general way, however, the data show that the inner temperatures of the maple-alder zone are lowered and the temperature extremes moderated, but the extremes in summer temperature much more so than those of the winter. The range in temperature is therefore more affected than the absolute temperatures. The importance of shade producers does not consist alone in their effectiveness to reduce transpiration, but also in their inverse influence upon meteorological factors.

The foregoing table also shows that the greater saturation deficiency was recorded for the station on the university campus. The relative evaporation in the three stations is according to the totals 1349.2 cc., 933.8 cc., and 690.8 cc., the corresponding ratios are 100, 69.2, and 51.2. These differences for the three stations remained fairly constant throughout. The fact that the evaporation rate for the central zone with its numerous xerophytes should be less than that for an area which supports mesophytic forest trees seems anomalous and surprising. Thus for the vegetation on the university campus the furtherance of transpiration by the evaporating power of the air is during some periods approximately two times greater than that on Cranberry Island. This clearly shows that the evaporating power of the air, though furnishing a very valuable criterion for the differentiation between great centers of plant distribution and for the differentiation of habitats, is not an important factor in controlling bog vegetation or determining the character of it.

With the data on hand, it is not difficult to see that the chief

TABLE VIII

VERTICAL EVAPORATION GRADIENT IN THE CRANBERRY-SPHAGNUM ZONE, CRANBERRY ISLAND

Date	Time	Light*	Anemometer; velocity in miles	Evaporation in cc.: cup at 3 in. (7.5 cm.) above ground	Temperature (C.); absolute, min.	max.	range	Evaporation in cc.: cup at 1 ft. (0.3 m.) above ground	Temperature (C.); absolute, min.	max.	range	Evaporation in cc.: cup at 5 ft. (1.5 m.) above ground	Temperature; absolute, min.	max.	range
July 30...	6 A.M.	sky clear	34.1	4.86	20	38	18	6.64	20	28	8	9.96	22.5	28	5.5
	12 M.	2 sec.													
	6 P.M.		25.1	11.34	21	37	16	14.94	24	32	8	19.92	26.5	29	2.5
July 31...	6 A.M.		3.6	0.00	8.5	27	18.5	0.00	8.5	27	18.5	1.66	11	28	17
July 31...	12 M.	8–9 sec.	18.1	3.24	16	34	18	6.64	18	30.5	12.5	9.13	17	27	10
July 31...	6 P.M.		12.7	6.48	22	42.5	20.5	7.47	21	30.5	9.5	10.37	24.5	28	3.5
Aug. 1...	6 A.M.		5.6	0.00	8	22	14	1.66	8	21	13	4.56	10.5	23.5	13
Aug. 1...	12 M.	7 sec.	12.1	4.05	15.5	35.5	20	6.64	18.5	32	13.5	7.47	16.5	28	11.5
Aug. 1...	6 P.M.		12	8.91	24.5	37	12.5	9.96	23.5	33.5	10	12.45	25.5	31.5	6
Aug. 2...	6 A.M.	sky clouded	5.4	0.00	13.5	24.5	11	0.00	13	23.5	10.5	2.49	11	31.5	20.5
Aug. 2...	12 M.	28 sec.	23.9	4.81	19	33.5	14.5	7.47	23	31	8	9.96	11	29.5	18.5
Aug. 2...	6 P.M.		25.7	5.67	25	34.5	9.5	7.47	24	32	8	10.19	25	30	5
Aug. 3...	6 P.M.	cloudy	85.1	14.58	19	37	18	21.58	15	37	22	28.22	17	35	18
Total evaporation				63.94				90.47				126.38			

*Time exposure at noon for sensitive photographic paper to standard tint.

external factor which exerts a direct influence on the evaporation at the bog island is the water area surrounding the island. Evaporation from the water surface and from the vegetation produces a vapor blanket, the action of which influences to a great extent the normal range of evaporation under the varying temperature conditions and consequently the rate of transpiration. The evaporation blanket is readily transported over the open central zone, its rate of movement and consequently the rate of evaporation varying particularly with the action of the wind. In the relatively forested maple-alder zone, however, the vapor blanket is more stationary and hence more uniform in its influence. This vapor blanket covers the locality to a definite height vertically. Studies on the phenomena of evaporation of water over lakes and reservoirs (**3**) have shown that the vapor pressure of the vertical gradient varies, beginning nearest the evaporating surface with a maximum, and rapidly diminishing within several feet above the evaporating surface, until it approximates to that in the free air. A few isolated readings confirmed this for the stations in question, as table VIII will show. At first the readings were taken every hour from 6 A.M. to 6 P.M.; later at intervals of six hours. For convenience, the larger time values covering the period from July 30 to August 3 are given here (fig. 8). The amounts are in the ratios 100, 71, and 50 for positions at 5 feet (1.5 m.), 1 foot (0.3 m.), and 3 inches (7.5 cm.), respectively. Hence in general, the lower stratum of a vegetation has a smaller range in humidity variations and possesses an atmosphere usually much more humid than the upper vegetation stratum or the free air above the vegetation level. The data confirm the noteworthy results of the evaporation experiments by YAPP (**34**), and show that the bog vegetation at the lower levels is exposed to transpiration conditions much less severe than those existing at positions above the substratum and those quite clear of vegetation.

But the growth of bog plants and their successful occupation of the habitat do not depend so much upon the total amount of evaporation or the time factor of this exposure, that is, the amount of moisture which the air contains during critical periods of the growing season. The functional activity of the plants is

not one of relation to a single factor. In the interrelation of conditions, the real limiting factor to an increase in functional activity is not evaporation or temperature, but the toxicity of the substratum. This fact reveals itself only in experimental tests. Toxicity comes markedly into play when the amount of water available for absorption has reached a stationary value, through

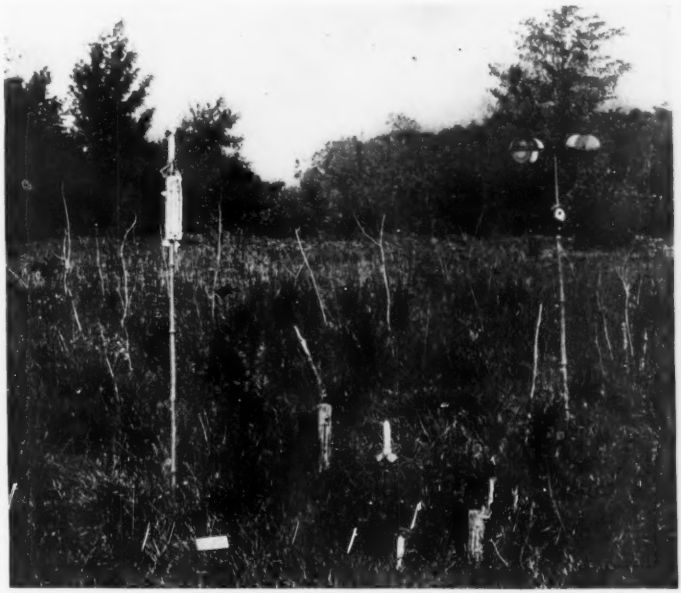

FIG. 8.—Experiment station in the cranberry-sphagnum association; in the foreground stunted growth of *Rhus Vernix;* photographed July 31, 1910.

the activity of bacterial organisms and other processes. In the field it is very difficult at times to decide which features of the vegetation are to be correlated with low atmospheric humidity, which with variations in temperature and light conditions, or with other factors cooperating at the same time. It is obvious that each in its turn may play the part of a limiting factor, for growth and transpiration are very susceptible to variations in either of these conditions. But in the laboratory the extended experi-

ments with cereals, legumes, and with plants from the various zones of the island have shown that most plants are unable to provide for a balanced relation between the supply of physiological water which the bog substratum can furnish and the excess of water lost during transpiration even when the temperature or the evaporating power of the air are favorable for any length of time. The susceptibility of the plants to the presence of small traces of deleterious bacterial transformation products accumulating in the surface layers of the peat substratum has been demonstrated elsewhere. An intimate and controlling relation has been found to exist between soil bacteria and the plants growing in the central zone. This has shown itself by various physiological and chemical tests, and by the fact that the presence and fitness of bog plants in the central zone is due mainly to more efficient functional responses to physiological drought. The edaphic aridity prevailing in this zone decreases the absorption of water by the roots in wheat plants about 50–65 per cent, at a time when transpiration and the growth of the plants demand a greater physiological water content. The further quotation of definite examples must be postponed. The ratio of the possible rate of water absorption to the rate of transpiration and growth becomes thus the real determining factor in the bog habitat and in the selection and in the distribution of plants. In all cases cultivated agricultural plants become flaccid and the roots appear gelatinous or as if burned black at the tips. The general dwarfing of roots (see illustrations in **7** and **8**) offers very little efficiency to physiologically arid conditions; nor is the change in form characters of shoot and leaf induced by the consequent lack of coordination of functions an advantage or an adaptation. Resistance to desiccation and the capacity for conserving water are more direct and more efficient responses to the limiting condition which the plants meet. This fact is not necessarily to be taken as valid in accounting for all highly specialized and inheritable structures so frequently met with in plants occurring in these habitats. The alteration of shoots and leaves in response to the stimulation of external factors may or may not increase fitness to the conditions, but it is safe to assume that the capacity for physiological changes and responses

controls the survival value of plant forms to a greater extent than has been admitted.

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BRIEFER ARTICLES

IS OPHIOGLOSSUM PALMATUM ANOMALOUS?

Under the unassuming title "Notes on the morphology of *Ophioglossum* (*Cheiroglossa*) *palmatum* L.," BOWER[1] has presented a paper containing generalizations of an unexpectedly far-reaching kind. Inasmuch as many of the arguments in this paper are directed against a paragraph in a recent paper by the present writer,[2] it seems desirable to make a few statements calculated to clear up the situation.

BOWER's account is based on two fertile specimens obtained during a visit to Jamaica, also on a reexamination of herbarium specimens. He adheres to his previous view of the morphology of the plant,[3, 4] namely, that the several to many fertile spikes are derived by duplication or branching of the single spike found in *O. vulgatum*, in contrast to the usual view that the spikes represent fertile lobes of the leaf. Probably the most serious objection to the latter interpretation is the fact, brought out by BOWER, that some specimens show one or more of the *distal* spikes inserted on the adaxial face of the leaf in a more or less median position, while one might expect to find them inserted marginally. Unfortunately neither of the specimens from Jamaica, and in fact no specimen which has been available for sectioning, shows this critical feature. BOWER recognizes the importance of this method of study, for in a number of his figures he represents the vascular supply of fertile spikes. I wish to point out that each of the cases so represented (figs. 17, i–ix; 19, i–v; 20, i–vii) fits in with my interpretation of the fertile spike as either a single segment of the leaf or a fused pair of segments, so I must insist that until an opportunity occurs for demonstrating the origin of the vascular supply to the upper median spikes, my interpretation stands. At the same time, I cheerfully admit the possibility of BOWER's view as an alternative theory, especially on the basis of the branching of fertile spikes, figured in 1896 for *O. pendulum* as well as *O. palmatum*. Is it

[1] Ann. Botany **25**: 277–298. *pls. 22–24.* 1911.

[2] The nature of the fertile spike in the Ophioglossaceae. Ann. Botany **24**: 1–18. *pls. 1, 2.* 1910.

[3] Studies in the morphology of spore-producing members. II. Ophioglossaceae. London. 1896.

[4] The origin of a land flora. London. 1908.

not possible, as has turned out in so many other cases, that the truth lies between the two extreme views? May it not be that the spikes of *O. palmatum* represent lobes of the leaf, and that certain of the upper ones in strong growing plants have suffered splitting or duplication? Such a view would take into account the effects of the peculiar life habits of this species, and at the same time would explain the identity in origin of the lower spikes with that found in the other members of the genus.

In his recent paper BOWER supports his interpretation by eight considerations, two of which are referred to above. Under one heading he urges the fact that "the identity of the margins of the leaf, so far as these are defined by the vascular strands, is entirely merged by the repeated fusions of the strands on the adaxial face of the elongated petiole" (p. 289). Yet, while describing the insertion of the petiolar strands on the central cylinder of the stem, BOWER shows that the leaf gap is obscured by a vascular commissure stretching across the gap at the point of attachment of the leaf trace bundles, and this fact does not cause a doubt as to the existence of a leaf gap. Apparently the anastomosing of vascular strands is characteristic of the plant, and the relationships of the parts can be best interpreted by comparison with simpler members of the family; this is what I have sought to do.

Professor BOWER'S caustic remarks concerning my paper on the Ophioglossaceae may the more readily be passed over in view of the fact that he has expressly repudiated his former view as to the relationships of the group, and hence accepts the main contention of my paper. With the candor characteristic of a true scientist, he has considered the evidence accumulated since 1896, and decides that the balance is in favor of allying the Ophioglossaceae with Filicales rather than with Lycopodiales. As a consequence of this, he regards the fertile spike not as a sporangiophore, but as one or more pinnae, here again agreeing with my conclusions. If now it is admitted that the fertile spike in most members of the group represents one pinna or a fused pair of pinnae, it is difficult for me to see why the interpretation should not be pushed to its logical end. The pinna nature of the fertile spike is most clearly seen in *Botrychium;* if the spike of *O. vulgatum* or *O. reticulatum* has a vascular supply which originates in a way similar to that of species of *Botrychium*, it may be regarded as representing two fused basal lobes of the leaf. The spike of *O. pendulum* has a similar vascular supply and may also be regarded as having the same morphological nature. A basal median spike in *O. palmatum* has a vascular supply identical with this; why then should it not be interpreted in the same way?

Marginal spikes situated above this would then represent single lobes of the leaf, comparable to the abnormal spikes of *B. obliquum* figured in my paper. In fact, the new figures representing sections through the base of fertile spikes more than ever convince me that there is an underlying unity in the family, in spite of the complications shown by *O. palmatum*. This unity appears in my interpretation of the fertile spike, and forms the only basis so far offered for comparison of all the members of the group.

Just what becomes of the order Ophioglossales remains slightly in doubt, for BOWER sometimes uses this term and sometimes the term Ophioglossaceae in his recent paper. Without entering into taxonomic considerations, it would appear that Ophioglossaceae might well remain a family of Filicales.

In conclusion it may be remarked that BOWER's admirable summing up of the differences in the vascular supply of spore-producing organs among the Psilotaceae, Sphenophyllaceae, and Ophioglossaceae lends support to the view that the two great phyla Lycopsida and Pteropsida have been separated for a vast period of time.—M. A. CHRYSLER, *University of Maine, Orono, Me.*

CRYPTOMERIA JAPONICA

(WITH FOUR FIGURES)

At the Harvard Botanic Garden, there is a *Cryptomeria japonica* 8–10 feet high. When examined early this spring, many of the branches that bore female cones were seen to have produced abnormal growths. The central axis of the cone had in some cases elongated into a vegetative branch. This condition has often been noted before in *Pinus*, *Abies*, *Larix*, *Sciadopitys*, and some other conifers, as well as in *Cryptomeria*. The *Gardeners Chronicle*[5] in discussing proliferous cones says, "this condition is so common in our experience as to be nearly as frequently met with as the normal state." Then again in reference to *Cryptomeria*,[6] "a very common peculiarity is the proliferation of the axis beyond the cone in the form of a slender branchlet." This vegetative proliferation has also been described by PENZIG,[7] MASTERS,[8] EICHLER,[9] and others.

Another and apparently undescribed condition was observed in the

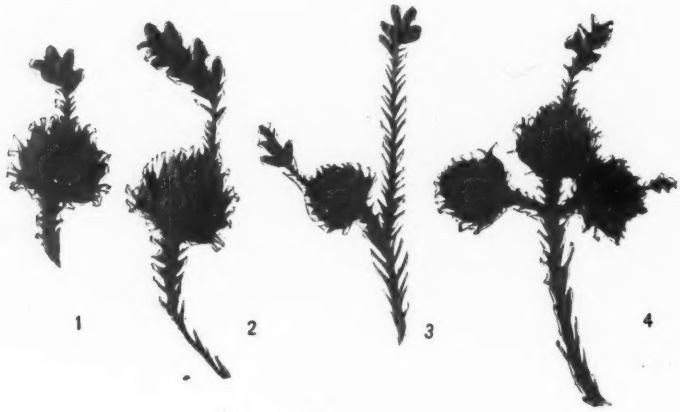
[5] Gard. Chron., January 28, 1882, p. 112. [6] *Ibid.*, November 30, 1901, p. 389.

[7] Pflanzen Teratologie, Vol. II, p. 509.

[8] Vegetable teratology, p. 245.

[9] Excursions morphological, Nat. Hist. Rev., April 1864.

case of the tree at the Botanic Garden. It was found in certain instances that the proliferating axis, instead of being merely a leafy shoot, bore male cones. This condition, so far as the writer has been able to observe, has not hitherto been described. Owing to repairs being made at the greenhouses, this tree had been placed horizontally in a dark pit for the winter. This unnatural condition perhaps accounted for the abnormal growths.



FIGS. 1–4

Figs. 1 and 2 show female cones bearing clusters of male cones on their elongated axes. Fig. 3 shows a normal cluster of male cones and another cluster on the proliferated female cone. Fig. 4 shows a normal female cone on the left, a female cone on the right bearing a vegetative branch, and a female cone in the center bearing a cluster of male cones.—ANSEL F. HEMENWAY, *Harvard University.*

CURRENT LITERATURE

BOOK REVIEWS

Plant pathology

The growing interest in plant pathology is attested by the appearance recently of two new books and a journal dealing with this subject. Of the books, one, by STEVENS and HALL,[1] is the second to appear in the United States within a year. The other, also in English, is by MASSEE.[2] The new journal appears under the name *Phytopathology*, as the official organ of the American Phytopathological Society.

The book by STEVENS and HALL is written to meet the needs of those who are concerned with plant diseases from a practical standpoint, and who wish to identify diseases easily and quickly, and find definite directions for combatting them. In its general scheme it departs considerably from the usual treatment adopted in works on plant diseases. The method of treatment is such as seemed to the writers most serviceable for the end in view. The diseased plant is the important object under discussion. Technical details relating to structure and life histories of fungi are omitted. Characteristics of fungi are described only where the fungus itself is sufficiently conspicuous to form a distinguishing mark by which to recognize the disease, as in mildews. Otherwise reference to the causal organism is limited to the giving of its scientific name after the common name of each disease. This enables one to identify the disease described. In the same way life histories are discussed only in so far as is necessary for the understanding of certain diseases, as in the case of rusts, and then only in their general aspects. In general only such characteristics are mentioned as are obvious to the naked eye and will aid the practical man in identifying the diseases. This method of treatment has permitted an arrangement of the material in the body of the work based on the classification of host plants, instead of the usual arrangement according to the systematic sequence of the fungi.

The book begins with brief introductory sections on general subjects of practical importance, such as fungicides, spraying machinery, cost and profits of spraying, and similar topics. This part is of special value to the practical man, as it brings together information regarding the newer spraying mixtures and methods of combatting diseases which have been published in various papers not easily available. A short chapter on general diseases takes up

[1] STEVENS, F. L., and HALL, J. G., Diseases of economic plants. 8vo. pp. x+513. *figs. 214.* New York: The Macmillan Co. 1910. $2.00.

[2] MASSEE, GEORGE, Diseases of cultivated plants and trees. 8vo. pp. xii+602. *figs. 171.* New York: The Macmillan Co. 1910. $2.25.

such diseases as "damping off," which are not restricted to particular species of plants. The rest of the book deals with "Special diseases of crops." The material is arranged according to the agricultural classification of plants, under such heads as pomaceous fruits, drupaceous fruits, small fruits, vegetable and field crops, cereals, fiber plants, trees and timber, and ornamental plants. The descriptions are clear and concise, giving such characteristics as enable the general reader to identify the disease. The book is illustrated by numerous halftones, which, however, are only of fair quality.

A feature peculiar to the book is the introduction of a unique popular nomenclature for the diseases described. This feature consists in the uniform construction of popular names, where none exist, by adding the ending -ose to the generic name of the organism causing the disease. Although this method of forming popular names has been used to some extent before by the authors and others, and consequently is not entirely an innovation here, it becomes conspicuous on account of the extent to which the idea is carried out. It is doubtful if such an arbitrarily constructed nomenclature can ever find wide acceptance, or if it is desirable; for popular names arise spontaneously, and have only local but forceful significance, which cannot be attained by names manufactured on a wholesale scale. In this case their acceptance would rather lead to a confusing monotony.

The book will be found extremely useful to those who have to do with the growing of plants. It will enable them readily to renew information on diseases known to them, and to identify new diseases not too obscure. Being alphabetically arranged, the book itself serves as a sort of host index, making the finding of material an easy matter. In each case is given what is known of methods of treatment, the matter of real importance to the grower.

The work of MASSEE is the outcome of the author's well-known *Text-book of plant diseases*, the last revised edition of which appeared in 1903. The growth of plant pathology in the interval has made necessary a complete revision of the text, with the addition of so much new material that the result is a new book. While it follows the general plan of the older work, the treatment of the subject is much more extended, owing partly to the enlarged scope of the new book, but more directly to the amount of new material incorporated and to the fuller treatment accorded to the individual subjects.

The book begins with introductory sections discussing such general subjects as primary and secondary causes of disease, epidemics, infection of plants, the dissemination of fungous diseases, injuries not due to fungi, and other related subjects. Space is also given to the discussion of fungicides and spraying. The American reader will be struck by the absence from this section of a discussion of apparatus for the application of fungicides.

The greater part of the book is taken up with descriptions of diseases and the fungi causing them. This part is arranged according to the groups of fungi, although none of the ordinary systems of classification are followed in detail. In the Pyrenomycetes, for example, the spore characters are taken

as the primary basis for the arrangement, thus leading to an association of genera entirely different from that usually found in taxonomic works. By this method of classification, the genera of the Hypocreales and Dothidiales are distributed among the Sphaeriales. In the descriptions both the characteristics of the diseases and the life histories and characteristics of the causal organisms are given. The scheme is similar to that followed in the author's *Text-book*, but the accounts are much more complete as to detail than those of the former work. In the last part of the book some of the diseases and injuries caused by animals are described. Notes on several diseases which could not be incorporated in the body of the work are appended in the addendum. The book is illustrated by halftones of drawings.

The work forms a useful handbook of general information on plant diseases. The older and better known facts receive full and careful treatment, but with regard to the newer facts of plant pathology, the work shows a lack of critical consideration of the literature which greatly impairs its value as a reliable reference book. A few instances illustrating this point may be cited. The rotting of lettuce in greenhouses is still attributed to *Botrytis cinerea* (*Sclerotinia Fuckeliana*) (p. 263), although the investigations of SMITH[3] several years ago have shown that *Sclerotinia Libertiana* is the principal cause of this rot, while *Botrytis*-forms are only of secondary importance. These two fungi, although related, differ greatly in their mode of life, *Botrytis* being a common saprophyte everywhere, while *S. Libertiana* is a soil fungus. This great difference in the mode of life of the two fungi is of importance when methods of combatting them are considered. The wilt disease of cotton and other plants is described (p. 228) under *Neocosmospora* (misspelled *Neocosmopara* in the page-heading, subject-heading, and text, and still different in the index). A symptom of the same disease is described (p. 494) under its old name "Cotton Frenching," caused by *Fusarium vasinfectum*. The genetic relationship between these two fungi has been shown by SMITH.[4] Spraying for peach leaf curl is regarded as of little value because the perennial mycelium of *Exoascus deformans* in the shoots produces a crop of diseased leaves each year in spite of spraying. As a matter of fact, there is no disease that can be controlled with more certainty and with more striking results by spraying than the peach leaf curl. Furthermore, the careful investigations of PIERCE[5] have shown that the origin of the spring infection is still obscure, but that probably the perennial mycelium in the branches has very little to do with the early infection. The common apple blotch fungus the author suggests

[3] SMITH, RALPH E., *Botrytis* and *Sclerotinia;* their relation to certain plant diseases and to each other. BOT. GAZETTE **29**:369–407. *pls. 3. figs. 3.* 1900.

[4] SMITH, ERWIN F., Wilt disease of cotton, watermelon, and cowpea. U.S. Dept. Agric., Div. Veg. Physiol. and Path., Bull. 17. 1899.

[5] PIERCE, NEWTON B., Peach leaf curl; its nature and treatment. U.S. Dept. Agric., Div. Veg. Physiol. and Path., Bull. 20. 1900.

(p. 412) is a stage of the apple scab fungus, yet these fungi could scarcely be confounded by one who had seen them. Under the heading "Peach leaf blotch (*Gloeosporium cydoniae* Mont.)," this disease is said to cause spots on the "living leaves of the peach (*Cydonia vulgaris*)." *Sphaeropsis malorum* is described only as a leaf spot disease of the apple, although it has been longest and best known as the cause of the black rot of the fruit, and later as the cause of a serious bark canker of apple trees.

The new journal *Phytopathology* is to be issued for the present as a bimonthly publication of the American Phytopathological Society. The aim, as set forth in the editorial announcement, is "to provide a place for the publication of phytopathological papers which would otherwise be lost or scattered in various places." While much of its space will be occupied by papers read before the society, it is the policy of the editors to make the journal more broadly representative and to open its pages to contributions of value from any source. It is of octavo size, containing at present about 35 pages of text and a number of plates in each issue. The halftone plates are of unusually good quality. The first issue is fittingly introduced by an excellent halftone portrait of DEBARY, with a brief sketch of his life and of the influence of his great personality on the advancement of plant pathology.

Heretofore the chief interest in plant pathology in the United States has been on its economic side, and this side has been highly developed as a result of the facilities for investigation, and for the ready means for publication of results having an economic bearing, offered by the experiment stations. As a result of the emphasis on the economic point of view, little attention has been given to the more fundamental problems relating to the subject. Such phases as the physiological relations between the host and parasite, the changes in metabolism brought about by the parasites, and the enzymatic activities of parasites, have remained almost uninvestigated. A journal like the present one, devoted entirely to the interests of plant pathology and not restricted to the purely economic phases of the subject, will undoubtedly do much to stimulate research in these deeper problems of plant pathology.—H. HASSELBRING.

Fossil plants

The second volume of SEWARD'S *Fossil plants*[6] has remained too long unnoticed by this journal. The first volume appeared in 1898, and the general purpose and method of the work were stated in the review published at that time.[7] The thirteen years that have elapsed have been memorable ones in the history of paleobotany, so that if this second volume had appeared as

[6] SEWARD, A. C., Fossil plants; a text-book for students of botany and geology. Vol. II. pp. xxii+624. *figs. 265*. Cambridge: The University Press; New York: G. P. Putnam's Sons. 1910. $5.00.

[7] Rev. in BOT. GAZETTE **26**:59. 1898.

promptly as at first expected, it would have been sadly out of date by this time. So large an addition has been made to our knowledge of fossil plants, that now we are to have three volumes of this work, instead of two, and the third volume, promised to appear "with as little delay as possible," is to contain the seed plants, and also a much-needed discussion of the geographical distribution of plants at different stages in the history of the earth.

The present volume contains the pteridophytes, with the exception of Equisetales and the major part of Sphenophyllales, which were treated in the first volume. As has been said often in this journal, the material of paleobotany must be traversed critically by morphologically trained paleobotanists, so that morphologists may be able to base their conclusions upon reasonably assured data. Even yet, most paleobotanists are stratigraphers, their chief concern being to be able to recognize a given horizon by a given form, whatever its relationships may be. Of course, such paleobotanists are geologists rather than botanists.

SEWARD has now done this service for botanists in the very critical series of fossil pteridophytes, and we are able to put together two or three competent and independent judgments, feeling well assured if we find agreement, and feeling cautious if we find disagreement. It is impossible to discuss the details of such a book, for it is more a manual than a reading text. It will be sufficient to indicate the titles of the 16 chapters.

XII, Sphenophyllales (continued) (16 pp.); XIII, Psilotales (13 pp.); XIV, Lycopodiales (62 pp.); XV, Arborescent Lycopodiales (104 pp.); XVI, Sigillaria (31 pp.); XVII, Stigmaria (21 pp.); XVIII, Bothrodendreae (23 pp.); XIX, Seed-bearing plants closely allied to members of the Lycopodiales (9 pp.); XX, Filicales (44 pp.); XXI, Fossil ferns (71 pp.); XXII, Marattiales (fossil) (17 pp.); XXIII, Psaronieae (15 pp.); XXIV, Ophioglossales (fossil) (5 pp.); XXV, Coenopterideae (91 pp.); XXVI, Hydropterideae and Sagenopteris (11 pp.); XXVII, Genera of Pteridosperms, ferns, and *plantae incertae sedis* (97 pp.).

These titles do not indicate any coordination, but perhaps they represent the legitimate state of mind in the presence of the material.—J. M. C.

MINOR NOTICES

New Zealand plants.—New Zealand is fortunate in having as its leading botanist one who has not only carefully studied the problems of plant life in a comparatively new region, but has now given to the general public a most interesting volume[8] on the vegetation of these islands. Beginning with a simple synopsis of the history of botanical explorations in New Zealand, from the work of Dr. JOHN FORSTER in 1773 to the present day, Dr. COCKAYNE proceeds to discuss the most notable features of a vegetation ranging from a

[8] COCKAYNE, L., New Zealand plants and their story. 8vo. vii+190. *figs.* 71. 1910. Wellington: John Mackay, Government Printer.

rain forest of almost tropical luxuriance to xerophytic sand dunes. The ecological viewpoint is maintained throughout, although the fact that the author is writing for a general audience seems to have led him from his usual scientific accuracy to many teleological interpretations. Still, the story of the New Zealand plants is told in so clear and interesting a manner that many botanists of other lands will find the little volume useful in imparting a picture of the vegetation of that distant country. For local use it cannot but be of the greatest service to teachers who are seeking an intelligent appreciation of their surroundings. The needs of the teaching profession are further recognized by a chapter on the cultivation of indigenous plants on the school grounds and in the school garden. The botanist will be interested, among other things, in the considerable number of plants with juvenile and adult leaf forms. The value of the volume is much increased by 70 illustrations from photographs of some of the most remarkable plants described.—GEO. D. FULLER.

North American Flora.[9]—Volume XXV, part 3, continues the treatment of the Geraniales and includes an elaboration of the Rutaceae and Surianaceae by PERCY WILSON, the Simaroubaceae by JOHN KUNKEL SMALL, and the Burseraceae by JOSEPH NELSON ROSE. New species, chiefly from Cuba and Mexico, are described in the following genera: *Ravenia* (1), *Zanthoxylum* (3), *Spathelia* (1), *Amyris* (1), *Elaphrium* (7), and *Icica* (10). One new genus (*Castelaria*) of the *Simaroubaceae* is proposed, based on *Castela Nicholsoni* Hook., to which are referred 8 species, 2 from Cuba being new to science.—J. M. GREENMAN.

Symbolae Antillanae.[10]—The publication of a third fascicle completes the sixth volume of Professor URBAN'S well-known work, *Symbolae Antillanae*. The fascicle recently issued continues the treatment of the Orchidaceae by A. COGNIAUX. There are recognized 96 genera, to which are referred 505 species, 28 being new to science. The excellent keys, careful and full descriptions, copious citation of exsiccatae, and complete synonomy with bibliography, make this a thoroughly scientific and standard work on the Orchidaceae of the Antillean region.—J. M. GREENMAN.

Handbook of deciduous trees.—The tenth part (fifth section of second volume) of SCHNEIDER'S *Handbuch* has just appeared,[11] the preceding part

[9] North American Flora, Vol. XXV, part 3, pp. 173–261. New York Botanical Garden. May 6, 1911.

[10] URBAN, I., Symbolae Antillanae seu fundamenta florae Indiae Occidentalis. Vol. VI, fasc., 3., pp. 433–721. Leipzig: Fratres Borntraeger. 1910.

[11] SCHNEIDER, C. K., Illustriertes Handbuch der Laubholzkunde. Zehnte Lieferung (fünfte Lieferung des zweiten Bandes). Imp. 8vo. pp. 497–757. *figs. 329–419*. Jena: Gustav Fischer. 1911. *M* 5.

having appeared in 1909.[12] It contains descriptions, with illustrations, of the angiospermous trees of central Europe, both native and under cultivation. The present part begins in the midst of *Rhododendron* and ends with *Viburnum*. —J. M. C.

NOTES FOR STUDENTS

Current taxonomic literature.—E. BRAINERD (Bull. Torr. Bot. Club **38**: 1–9. *pl. 1.* 1911) presents an article entitled "Further notes on the stemless violets of the South," and describes two new varieties.—R. E. BUCHANAN (Mycologia **3**:1–3. *pls. 34, 35.* 1911) describes and illustrates a new hyphomycete (*Thyrococcum humicola*), obtained from pure cultures.—C. DE CANDOLLE (Phil. Journ. Sci. Bot. **5**:405–463. 1910) presents "A revision of Philippine Piperaceae" in which he recognizes 22 species of *Peperomia* and 123 of *Piper*. Of the total number about 50 are new to science.—J. CARDOT (Rev. Bryol. **38**:33–43. 1911) under the title "Diagnoses préliminaires de Mousses mexicaines" has published several new species of mosses, based mainly on collections made in southern Mexico by C. R. BARNES and W. J. G. LAND in 1908.—C. CHRISTENSEN (Arkiv för Bot. **10**[2]:1–32. *pl. 1.* 1910) presents an article "On some species of ferns collected by Dr. CARL SKOTTSBERG in temperate South America" in 1907–1909. The paper includes descriptions of 3 species new to science.—W. N. CLUTE (Fern Bull. **18**:97, 98. 1910) describes and illustrates a new species of *Polypodium* (*P. prolongilobum*) and a new variety of *P. vulgare* L. from Arizona.—E. B. COPELAND (Leafl. Phil. Bot. **3**:791–851. 1910) enumerates upward of 250 species of ferns from Mount Apo, Philippine Islands; of this number 16 are described as new. The author states: "It is probable that this is the richest known fern flora in the world." *Polypodium* and *Dryopteris* are the predominating genera.—A. D. E. ELMER (Leafl. Phil. Bot. **3**:853–1107. 1910–1911) records further data concerning the flora of the Philippine Islands, and describes 138 species of flowering plants as new.—M. L. FERNALD (Rhodora **13**:4–8. 1911)has published a new species of *Scirpus* (*S. Longii*) from Massachusetts and New Jersey.—D. GRIFFITHS (Rep. Mo. Bot. Gard. **21**:165–175. *pls. 19–28.* 1910) in continuation of his studies on the genus *Opuntia* has described and illustrated 10 new species indigenous to southwestern United States and northern Mexico.—E. HASSLER (Rep. Nov. Sp. **9**:1–18, 49–63, 115–121. 1910–1911) has published several new species, varieties, and forms in the genus *Mimosa* and in the families Bignoniaceae and Solanaceae from Paraguay. One new genus (*Rojasiophyton*) of the Bignoniaceae is proposed.—F. D. HEALD and F. A. WOLF (Mycologia **3**:5–22. 1911) have published 41 new species of Texan fungi.—A. A. HELLER (Muhlenbergia **7**:1–11, 13–15. 1911) records further results of his studies on "The North American lupines" and describes two new species: *L. sabulosus* from the sand hills near San Francisco and *L. apodotropis* from Oregon.—A. F. G. KERR and W. G. CRAIB (Kew Bull. 1–60. 1911) under the general title of

[12] BOT. GAZETTE **48**:312. 1909.

"Contributions to the flora of Siam" have issued an interesting paper on the little known flora of that region. A general sketch of the vegetation is from the pen of Dr. KERR, and a "List of Siamese plants with descriptions of new species" is the work of Mr. CRAIB. Several new species are added to the flora and one new genus (*Pittosporopsis*) of the Icacinaceae is proposed.—W. LIPSKY (Acta Hort. Petrop. **26**:119–616. *pls. 3–6.* 1910) continues his important publications on the flora of central Asia. The present contribution contains descriptions of several new species, particularly in *Astragalus* and *Potentilla*. The treatment of the latter genus was contributed by the noted specialist TH. WOLF.—T. H. MACBRIDE (Mycologia **3**:39, 40. *pl. 36.* 1911) describes and illustrates a new genus (*Schenella*) doubtfully referred to the Myxomycetes. The material on which the genus is based was found growing on a decaying pine log in the Yosemite Valley, California.—M. E. MCFADDEN (Univ. Calif. Pub. Botany **4**:143–150. *pl. 19.* 1911) presents an account of "A Colacodasya from southern California," and in conjunction with Dr. W. A. SETCHELL describes a new species (*C. verrucaeformis*) found growing on *Mychodea episcopalis* J. Ag.—E. D. MERRILL and M. L. MERRITT (Phil. Journ. Sci. Bot. **5**:371–403. *pls. 1–4. 1 map.* 1910) in a concluding article on "The flora of Mount Pulog" have published 11 new species of Sympetalae. Two new genera are described by Mr. MERRILL, namely *Loheria* of the Myrsinaceae and *Merrittia* of the Compositae.—W. A. MURRILL (Mycologia **3**:23–36, 79–91. 1911) has issued the first two papers of a proposed series of articles on "The Agaricaceae of tropical North America," recording new species in *Leucomyces*, *Limacella*, *Russula*, *Lentinus*, and *Lepiota*.—G. E. OSTERHOUT (Muhlenbergia **7**:11, 12. 1911) describes a new species of *Schmaltzia* (*S. pubescens*) and one of *Carduus* (*C. vernalis*) from Colorado.—F. W. PENNELL (Torreya **11**:15, 16. 1911) records a new species of *Gerardia* (*G. racemulosa*) from New Jersey.—C. B. ROBINSON (Phil. Journ. Sci. Bot. **5**:465–543. 1910) begins a monographic consideration of the "Philippine Urticaceae," treating 9 genera to which are referred 86 indigenous species, about one-half being new to science. One new genus (*Elatostematoides*) is proposed.—E. ROSENSTOCK (Rep. Nov. Sp. **9**:67–76. 1910) has published 16 new species of ferns, 5 of which are from Costa Rica.—P. A. RYDBERG (Bull. Torr. Bot. Club **38**:11–23. 1911) in continuation of his "Studies on the Rocky Mountain flora" has described several new species of Compositae.—G. SCHELLENBERG (Mitt. Bot. Mus. Univ. Zürich, No. 50, pp. 1–158. 1910) under the title "Beiträge zur vergleichenden Anatomie und zur Systematik der Connaraceen" has published the results of a detailed study of this family, recognizing 17 genera and over 100 species. One new genus (*Santaloides*), based on *Rourea Afzelii* Planch. from Africa, is new to science.—A. K. SCHINDLER (Rep. Nov. Sp. **9**:123–125. 1911) under the title "Halorrhagaceae novae I" includes two new species of *Gunnera* from Peru.—R. SCHLECHTER (*ibid.* 21–32) has published 20 new species of orchids, 13 of which are from Central and South America.—F. J. SEAVER (Mycologia **3**:57–66. 1911) publishes the results of studies in Colorado fungi and includes descriptions of

two new species, namely *Ascobolus xylophilus* and *Godronia Betheli*.—D. R. SUMSTINE (*ibid.* 45–56. *pls. 37–39*) under the title of "Studies in North American Hyphomycetes I" presents a taxonomic treatment of *Rhinotrichum* and *Oliptrichum*, recognizing for the former 13 species, of which 3 are new to science.—F. THEISSEN (Broteria, Ser. Bot. **9**:121–147. *pls. 5–9.* 1910) in an article entitled "Hypocreaceae Riograndensis" has published 15 new species. The same author (Beih. Bot. Centralbl. **27**[2]:384–411. 1910) under the title "Fungi Riograndensis" lists about 150 species from southern Brazil, 10 of which are new to science. One new genus (*Creosphaeria*) is characterized and is said to be intermediate between *Rosellinia* and *Hypoxylon*.—I. TIDESTROM (Am. Mid. Nat. **1**:165–171. *pl. 11.* 1910) has published 3 new species of *Aquilegia* from western United States and gives a synopsis of 10 recognized species.—I. URBAN (Ber. Deutsch. Bot. Gesell. **28**:515–523. *pl. 15.* 1911) has published a new species of *Loasa* (*L. Plumeri*) and a new monotypic genus (*Fuertesia*) of the Loasaceae from Sto. Domingo.—W. WEINGART (Monats. für Kakteenkunde **21**:5–7. 1911) describes a new species of *Phyllocactus* (*P. Eichlamii*) from Guatemala.—R. S. WILLIAMS (Bull. N.Y. Bot. Gard. **6**:227–261. 1910) under the title "Bolivian Mosses, Part II," has described 18 new species. The same author (Bull. Torr. Bot. Club **38**:33–36. 1911) records two new species of mosses from Panama.—N. N. WORONICHIN (Bull. Jard. Imp. Bot. St. Petersb. **11**:8–19. 1911) records a list of fungi collected in southeastern Russia, and includes a new ascomycetous genus (*Rhodosticta*) parasitic on the leaves of *Caragana frutex* Koch.—J. M. GREENMAN.

The number of chromosomes.—In 1909 STRASBURGER made a cytological study of the parthenogenetic *Wikstroemia indica*, and now he has succeeded in securing from the rather inaccessible Himalaya region material of the nearly related *W. canescens*, in which fertilization regularly occurs. From an investigation of *W. canescens* and a study of the literature of forms with unexpectedly large numbers of chromosomes, some interesting conclusions are reached.[13]

High chromosome numbers can be shown to be the result of multiplication of whole chromosomes, so that the organism becomes polyploid, with a diploid gametophyte and tetraploid sporophyte, instead of the usual haploid and diploid generations. Such increases in chromosome numbers must be referred to mitotic division, which does not get to the separation of the daughter chromosomes, or, if daughter nuclei are formed, they reunite. The increase in number comes usually from a longitudinal division, which gives like products, and it is probable that the phenomenon takes place in the fertilized but not yet divided egg. The increase in the number of chromosomes is accompanied by some increase in the size of the nucleus and protoplast.

In the nuclei of sporophytes which are more than diploid, the homologous

[13] STRASBURGER, EDUARD, Chromosomenzahl. Flora **100**:1–50. *pl. 6.* 1910.

chromosomes are grouped in pairs, and not in tetrads in tetraploid nuclei. In the triploid nuclei of the endosperm of angiosperms, there are both paired and unpaired chromosomes. In the mother cells of polyploid plants there are always only bivalent chromosomes (gemini), and never a complex of more than two chromosomes as elements of the reduction plate. In triploid nuclei of the sporophyte of hybrids which result from a union of haploid and diploid gametes, there are both paired and single chromosomes, and in the mother cells of such plants both paired and single chromosomes appear. From a study of the various pairings it seems that they depend upon an attraction between homologous chromosomes, so that this homology, rather than any maternal or paternal origin, determines the formation of pairs, and it may be possible that a pair of two homologous chromosomes may be derived from the same sex product. The increase in the number of chromosomes has often led to parthenogenesis (*eiapogamy*), but there is also parthenogensis without any increase in the number of chromosomes.

The large number of chromosomes does not always result from longitudinal division, but may be due to a transverse division, and in this case there is no increase in the size of the nucleus and no loss of sex occurs. Zoological literature shows many instances of analogous phenomena.

This paper suggests a wide range of problems for cytological investigation, and obviously it has an important bearing upon the theory of the individuality of the chromosome.—CHARLES J. CHAMBERLAIN.

Sixteen-nucleate embryo sacs.—The ovule of *Euphorbia procera*[14] has several hypodermal archesporial cells, each of which divides into a tapetal cell and a megaspore mother cell. The two reduction divisions take place in the mother cells, but are not accompanied by wall formation, so that each megaspore mother cell now contains four megaspore nuclei, or rather, four megaspores not separated by walls. At this stage all the tetrads degenerate except one, and in this each megaspore nucleus undergoes two successive mitoses, giving rise to a 16-nucleate sac. Several other species of *Euphorbia* were examined, and all had a single archesporial cell and a typical 8-nucleate sac.

MODILEWSKI[15] had previously shown that in the 16-nucleate stage of *E. procera* the nuclei are arranged in four tetrad-like groups, from each of which one nucleus moved to the center of the sac to form the endosperm nucleus. The micropylar group formed the egg apparatus and the chalazal group the antipodals, while the two lateral groups resembled the egg apparatus. Double fertilization was observed, the second male nucleus fusing with the four nuclei at the center of the sac, so that the endosperm nucleus resulted from the fusion of five nuclei. The chromosome situation was not determined.

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[14] MODILEWSKI, J., Weitere Beiträge zur Embryobildung einiger Euphorbiaceae. Ber. Deutsch. Bot. Gesell. **28**:413–418. *pl. 12*. 1910.

[15] ———, Zur Embryobildung von *Euphorbia procera*. Ber. Deutsch. Bot Gesell. **27**:21–26. *pl. 1*. 1908.

MODILEWSKI[16] has also described a 16-nucleate embryo sac in *Gunnera chilensis*, in which case the four megaspores, not separated by walls, all take part in forming the embryo sac. Although no definite proof was obtained, he believed the embryos to be parthenogenetic.

An interesting embryo sac is described by DESSIATOFF,[17] who finds 16 nuclei in *Euphorbia virgata* at the fertilization period. The 16 nuclei come from one megaspore, and consequently the situation is somewhat different from that found in *Peperomia*, where 4 megaspores enter into the formation of the sac. The 16 nuclei are arranged in four groups of four each, and one nucleus from each group moves to the center of the sac, where the four fuse to form the endosperm nucleus. There are three antipodals, and an egg apparatus of two synergids, and an egg. The two other groups remain at the side of the sac and resemble the egg apparatus. In general, this embryo sac resembles that of the Penaeaceae as described by Miss STEPHENS.—CHARLES J. CHAMBERLAIN.

The sperm nuclei of Lilium.—Since zoological literature furnishes no instance of the fertilization of the egg by a naked male nucleus unaccompanied by any cytoplasm, and since the male nucleus in plants has in nearly all cases been shown to be accompanied by cytoplasm, definite proof of fertilization by a naked nucleus is worth recording, especially since the nucleus is regarded by many as the sole bearer of hereditary qualities. Both STRASBURGER and KOERNICKE have claimed that in *Lilium* the sperm nucleus, at the time of fertilization, is not accompanied by any cytoplasm. A paper by NAWASCHIN,[18] the discoverer of double fertilization, gives a very complete account of the generative cell and development of the sperm nuclei in the classic *Lilium Martagon*. The excellent technic, remarkably close series of stages, and the carefully drawn illustrations, all support NAWASCHIN'S description and conclusions. The cytoplasm of the generative cell has a finely granular structure up to the anaphase of the division of its nucleus, at which time its cytoplasm begins to mingle with the general cytoplasm of the pollen tube. The mitosis which gives rise to the two male nuclei is characterized at every stage by sharply differentiated chromosomes, so that the sperm nuclei do not reach the resting stage, but remain in the condition characteristic of telophase. Consequently, it is not improbable that the mature nuclei are capable of movement. The achromatic spindle is scanty and in some cases doubtful, and in others cannot be identified at all, so that it is probable that

[16] MODILEWSKI, J., Zur Embryobildung von *Gunnera chilensis*. Ber. Deutsch. Bot. Gesell. **26a**:550–556. *pl. 11*. 1908.

[17] DESSIATOFF, N., Zur Entwickelung des Embryosackes von *Euphorbia virgata*. Ber. Deutsch. Bot. Gesell. **29**:33–39. *figs. 17*. 1911.

[18] NAWASCHIN, SERGIUS, Näheres über die Bildung der Spermakerne bei *Lilium Martagon*. Ann. Jard. Bot. Buitenzorg. II. Supplement III. 871–904. *pls. 33, 34*. 1910.

the chromosomes in this mitosis move independently of any spindle.—C. J. CHAMBERLAIN.

Studies in ferns.—Apogamy in *Cystopteris fragilis*, hybridization in *Asplenium*, and conditions of heredity in certain ferns, have been investigated by A. HEILBRONN.[19] The group last considered includes, as true varieties, the following: *Aspidium Filix-mas* var. *grandiceps*, *A. aculeatum* var. *cruciato-polydactylum*, *Athyrium Filix-femina* var. *corymbiferum*, *A. Filix-femina* var. *multifidum*, *A. Filix-femina* f. *multifidum Mapple-Beckii*, *A. Filix-femina* var. *laciniatum* and var. *purpureum* Lowe. Others not considered true varieties are *Athyrium Filix-femina* var. *Fieldiae* Moore, *A. Filix-femina* f. *multifidum minus*, and *Aspidium angulare* f. *grandidens*. The general conclusions of the author are: (1) *Cystopteris fragilis* f. *polyapogama* develops prothallia which show the power of developing sporophytes from unfertilized egg cells or by vegetative apogamy, the two cases sometimes being side by side; (2) the question as to whether *Asplenium germanicum* is a hybrid between two forms is not yet settled, but by crossing *Asplenium septentrionale* (female) and *A. Ruta-muraria* (male), a plant was obtained which stands nearer to *A. germanicum* than any other known form; (3) some fern-forms which had not been investigated before appear apogamous. Of the different forms of *Athyrium Filix-femina* from England, some are true varieties and some revert. Attempts to obtain forkings artificially were unsuccessful.—NORMA E. PFEIFFER.

Water-cultures of fern prothallia.—In a short paper H. FISCHER[20] gives some of his results with the germination of fern spores, in obtaining material for his work on variation, hybridization, etc. He states the advantages of water-cultures over solid substrata as being threefold: the chemical constitution can be regulated; the cultures are cleaner, and material is fit for microtome sections without extra care; the spores may be sowed as thick as desirable, and easily diluted, like a solution, if too close together on germination. The danger lies in the drying out of cultures, or too great evaporation, resulting in plasmolysis. A second danger lies in the production of abnormal forms by too deep layers. The author recommends Pfeffer's nutrient solution and Arthur Meyer's solution, the formula of which he gives. He finds that changing one compound or its concentration, changing the reaction of a solution, etc., often produce the desired germination. But evidently there is no general rule for this, as there is none for the length of time after ripening that a spore will germinate. In *Asplenium Serra*, herbarium material germinated after 48 years. In some few cases the author is as yet unable to induce germination.—NORMA E. PFEIFFER.

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[19] HEILBRONN, ALFRED, Apogamie, Bastardierung, und Erblichkeitsverhältnisse bei einigen Farnen. Flora (n.s.) **1**: 1–42. *figs. 43*. 1910.

[20] FISCHER, HUGO, Wasserkulturen von Farnprothallien, mit Bemerkungen über die Bedingungen der Sporenkeimung. Beih. Bot. Centralbl. **27**[1]: 54–59. 1911.

Development of banana pollen.—An extensive investigation[21] of three races of the edible banana (*Musa sapientum*) has shown that they can be distinguished by the number of chromosomes, "*Dole*" having 8, "Radjah Siam" 16, and "Kladi" 24, as the haploid numbers, so that the races might be designated as vars. *univalens*, *bivalens*, and *trivalens*. The volume of the nuclei, but not their surfaces, is in the ratio 1:2:3. With the increase in the number of chromosomes came disturbances in the development of pollen, some of the chromosomes not passing to the poles, but remaining behind and forming extra nuclei. The size of the tetrad varies in a given anther, although the number of chromosomes in the entire tetrad is constant. Sometimes as many as eight pollen grains are formed from a single mother cell.

Prochromosomes are easily distinguished in the pollen mother cell, and in *Musa Dole* TISCHLER was able to show that the number of prochromosomes was equal to the diploid number of chromosomes. Probably there is a fusion of prochromosomes at synapsis. The splitting of chromosomes at the strepsonema stage TISCHLER regards as genuine and not merely apparent.—CHARLES J. CHAMBERLAIN.

Parthenogenesis in Taraxacum.—Parthenogenesis in *Taraxacum* has been investigated again, this time by SCHKORBATOW[22] who writes in Russian, but adds a summary in German, from which the following points are taken: The removal of anthers does not in any way affect the germination of seeds. Various colors of seeds, like clear green and dark brown, may become fixed and hereditary. At metaphase of the first division in the embryo sac, the chromosomes show various and characteristic forms, but the chromosomes seldom take the arrangement belonging to the heterotypic mitosis, and when they do, the author regards the phenomena as atavistic. Amitotic divisions occur in the embryo sac, in the endosperm, and in early stages of the embryo, in the last case all the nuclei but one becoming resorbed, so that the cells are left uninucleate.—CHARLES J. CHAMBERLAIN.

The origin of the vacuole.—Probably most botanists believe that the large vacuoles of plants arise by the coalescence of numerous smaller ones. A paper by BENSLEY,[23] dealing with the canalicular apparatus of animals, gives also a description of root tips and the tapetum of anthers. The fixing agent used was: neutral formalin (freshly distilled), 10 cc.; water, 90 cc.; potassium bichromate, 2.5 g.; mercuric chloride, 5.0 g. With this fixing

[21] TISCHLER, G., Untersuchungen über die Entwickelung des Bananen-Pollens. I. Archiv. für Zellforschung **5**:622–670. *pls. 30, 31.* 1910.

[22] SCHKORBATOW, L., Parthenogenetische und apogame Entwickelung bei den Blüthenpflanzen. Entwickelungsgeschichtliche Studien an *Taraxacum officinale* Wigg. Bot. Institut Charkow. pp. 43. *pl. 1. figs. 4.* 1910.

[23] BENSLEY, R. R., On the nature of the canalicular apparatus of animal cells. Biol. Bull. **19**:174–194. *figs. 1–3.* 1910.

agent and Haidenhain's iron alum haematoxylin, or Flemming's triple stain, the young cells, especially of the dermatogen and plerome, show an intricate network of canals, and older cells show a gradual transition from the network, which is a single structure, to the familiar appearance obtained by current methods. This method promises to solve the problem of the origin of the vacuole, and at the same time it is excellent for nuclear structures.—CHARLES J. CHAMBERLAIN.

Mitochondria.—The small bodies variously known as mitochondria, chondriosomes, chondriokonten, and chromidial substance, have been known to zoologists for some time, but it is only recently that they have attracted any serious attention among botanists. A short paper by LEWITSKI[24] describes the mitochondria in young cells of *Pisum sativum* and *Asparagus officinale*. In the root tip the mitochondria become transformed into leucoplasts, and in the stem tip into chloroplasts. The mitochondria divide and are believed to be an essential part of the cytoplasm. No mitochondria were found inside the nucleus, and the author does not believe that there is any passage of mitochondria between nucleus and cytoplasm. Division of mitochondria is figured and described.—CHARLES J. CHAMBERLAIN.

Origin of the plastid.—For nearly twenty years the theory that the plastid is a permanent organ of the cell, arising only by the division of a preexisting plastid, has been generally accepted, doubtless on account of the thorough investigations of SCHIMPER and of MEYER. When LEWITSKI's paper appeared, claiming that plastids arise from chondriosomes, MEYER[25] at once denied the claim and demanded proof. For several years the reviewer has doubted the accuracy of the conclusion reached by both SCHIMPER and MEYER that the plastid arises only by the division of a pre-existing plastid. Their evidence seems more voluminous than convincing. It is to be hoped that this incipient controversy will settle the status of the plastid.—CHARLES J. CHAMBERLAIN.

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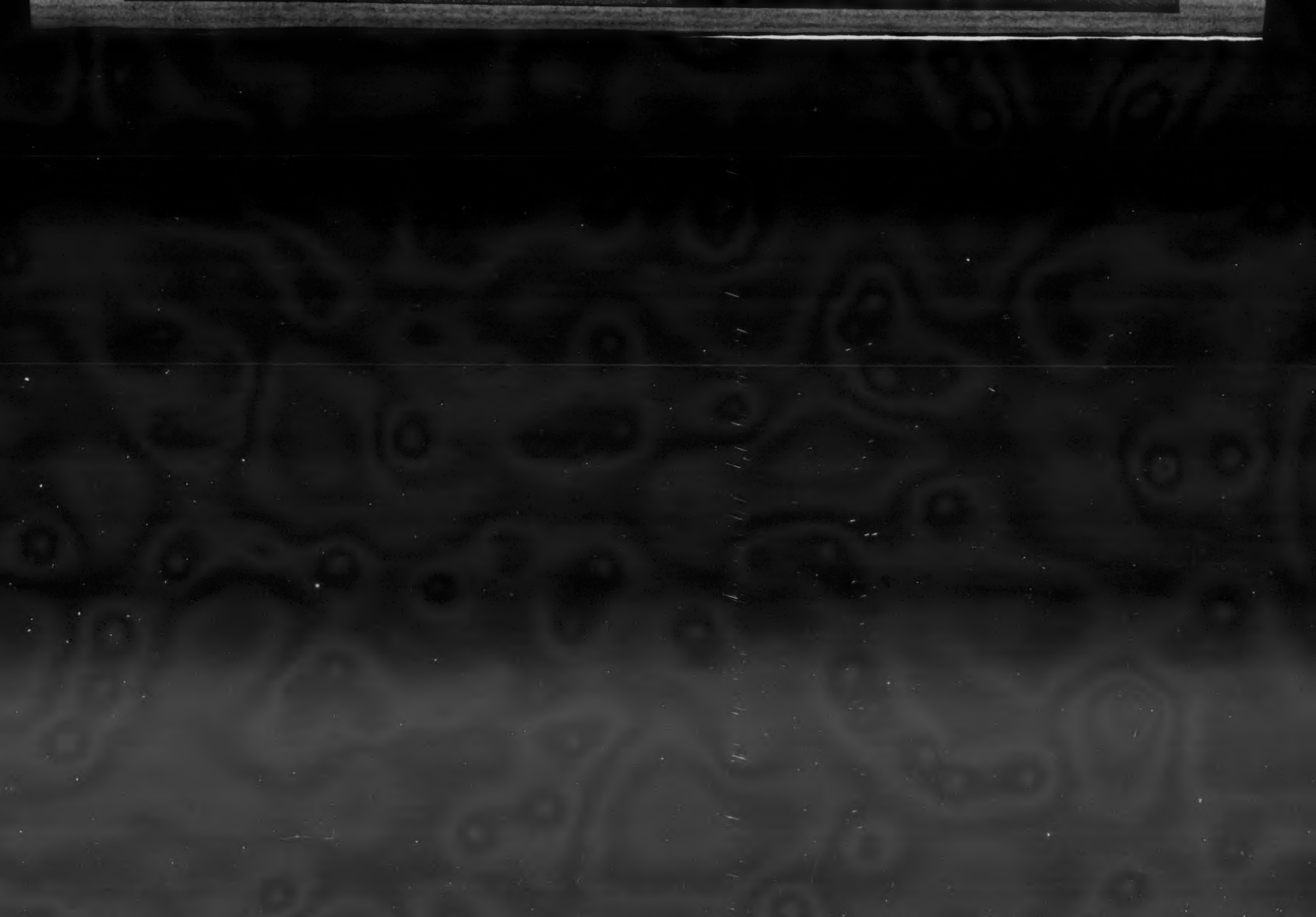
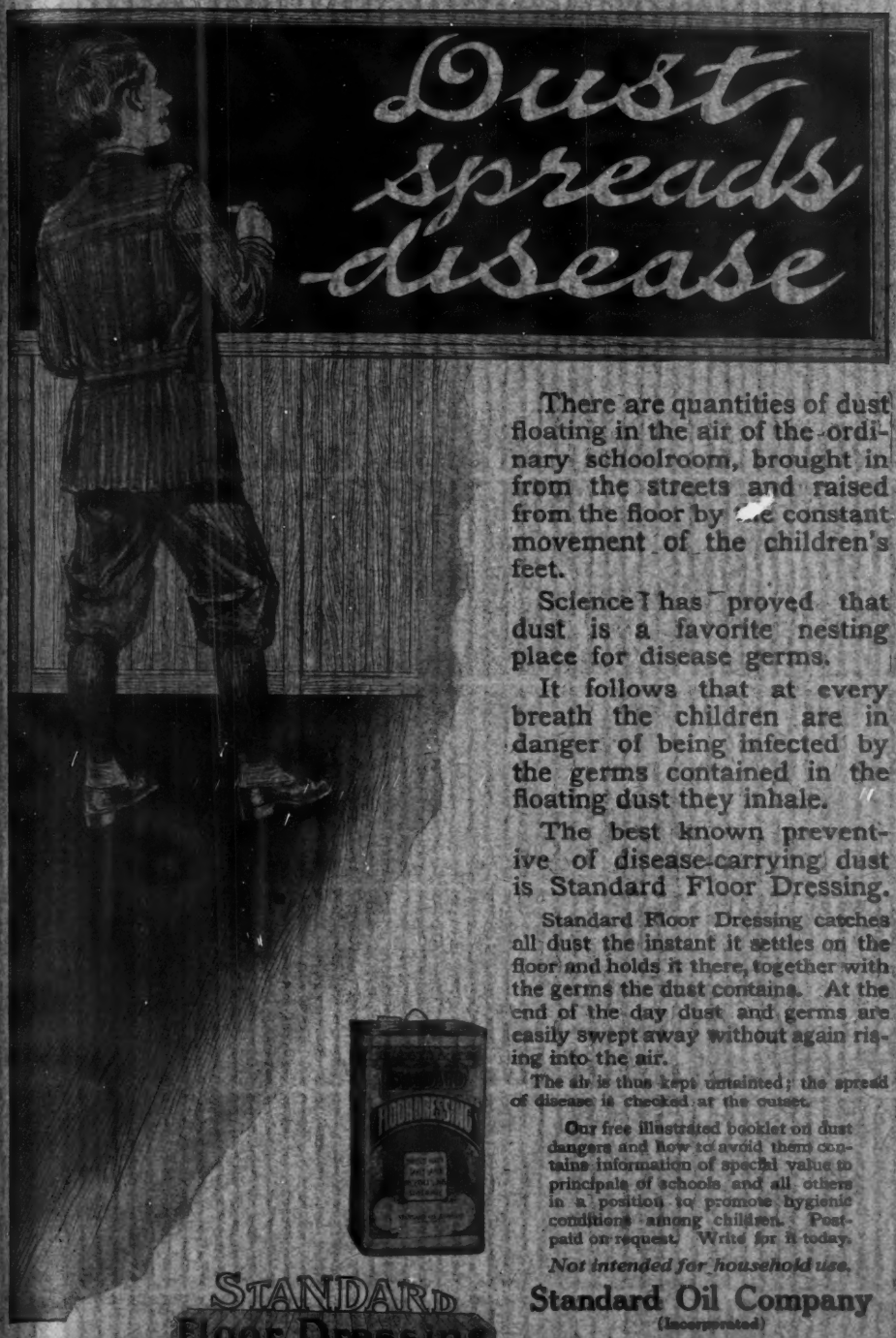
[24] LEWITSKI, G., Ueber die Chondriosomen in pflanzlichen Zellen. Ber. Deutsch. Bot. Gesell. **28**:538–546. *pl. 17*. 1910.

[25] MEYER, ARTHUR, Bermerkungen zu G. LEWITSKI: Ueber die Chondriosomen in pflanzlicher Zellen. Ber. Deutsch. Bot. Gesell. **29**:158–160. 1911.





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